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Stock Structure of Scotian Shelf Flatfish as Inferred from Ichthyoplankton Survey Data and the Geographic Distribution of Mature Females

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Neilson, J. D., E. M. DeBlois, and P. C. F. Hurley. 1988. Stock structure of Scotian Shelf flatfish as inferred from ichthyoplankton survey data and the geographic distribution of mature females. Can. J. Fish. Aquat. Sci. 45: 1674–1685.

Data on egg distributions and timing of appearance of maximum egg densities were examined to determine the stock structure of three commercially important flatfish occurring on the Scotian Shelf: American plaice (*Hippoglossoides platessoides*), yellowtail flounder (*Limanda ferruginea*), and witch flounder (*Glyptocephalus cynoglossus*). Distributions of sexually mature females obtained from research vessel surveys were used to further support inferences concerning spawning location. Using such information, more than one stock of both American plaice and yellowtail flounder appear to occur on the Scotian Shelf, but no conclusions could be drawn concerning witch flounder. In the case of American plaice and yellowtail flounder, the existing means of geographic aggregation of data for stock assessment purposes do not appear to adequately represent stock structure. Little or no advection of eggs and larvae appears to occur on the Scotian Shelf, supporting the hypothesis that current-driven retention areas promote stock discreteness in that region. It was concluded that ichthyoplankton surveys can be a valuable adjunct to more traditional means of stock identification.

Les auteurs ont examiné les répartitions des oeufs et le moment d'apparition des densités maximales d'oeufs pour déterminer la structure des stocks de trois espèces de poissons plats importantes sur le plan commercial que l'on rencontre sur la plate-forme Scotian, soit la plie canadienne (*Hippoglossoides platessoides*), la limande à queue jaune (*Limanda ferruginea*) et la plie grise (*Glyptocephalus cynoglossus*). Ils se sont servis des répartitions des femelles ayant atteint la maturité sexuelle, obtenues de relevés de navires de recherche, pour étayer davantage les déductions concernant les aires de frai. Selon ces informations, il semble y avoir plus d'un stock de plie canadienne et de limande à queue jaune sur la plate-forme Scotian, mais on n'a pu tirer de conclusions pour la plie grise. Dans le cas de la plie canadienne et de la limande à queue jaune, les moyennes actuelles de concentration géographique des données ne semblent pas représenter adéquatement la structure des stocks. Il semble y avoir peu ou pas de déplacement d'oeufs et de larves sur la plate-forme Scotian, ce qui appuie l'hypothèse voulant que les zones de rétention dues aux courants favorisent le caractère distinct des stocks dans cette région. Les auteurs en arrivent à la conclusion que les relevés d'ichtyoplancton peuvent être un complément valable des méthodes plus traditionnelles d'identification des stocks.

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A stock has been defined as a population of fish that maintains Castle–Hardy–Weinberg equilibrium within certain temporal and spatial limits (Booke 1981). Fishery management units based on stock structure provide a means for the maintenance of such equilibria when outside influences such as exploitation become a significant pressure on the population. Without carefully chosen management units, particularly where the fishery consists of more than one stock, there is a risk of overharvesting less abundant components, which could lead to lower total yield and loss of genetic diversity (Altukhov 1981). Indeed, stock definition is increasingly being viewed as a necessary first step towards the goal of rational fishery management (Kutkuhn 1981).

A number of criteria are available which allow fisheries managers to identify management units consistent with stock structure. They include examination of the distribution of the fishery, location of spawning areas, values of population parameters (such as growth and mortality rates), morphological and physiological characteristics, and movements and migrations as determined through marking programs (Gulland 1983). The

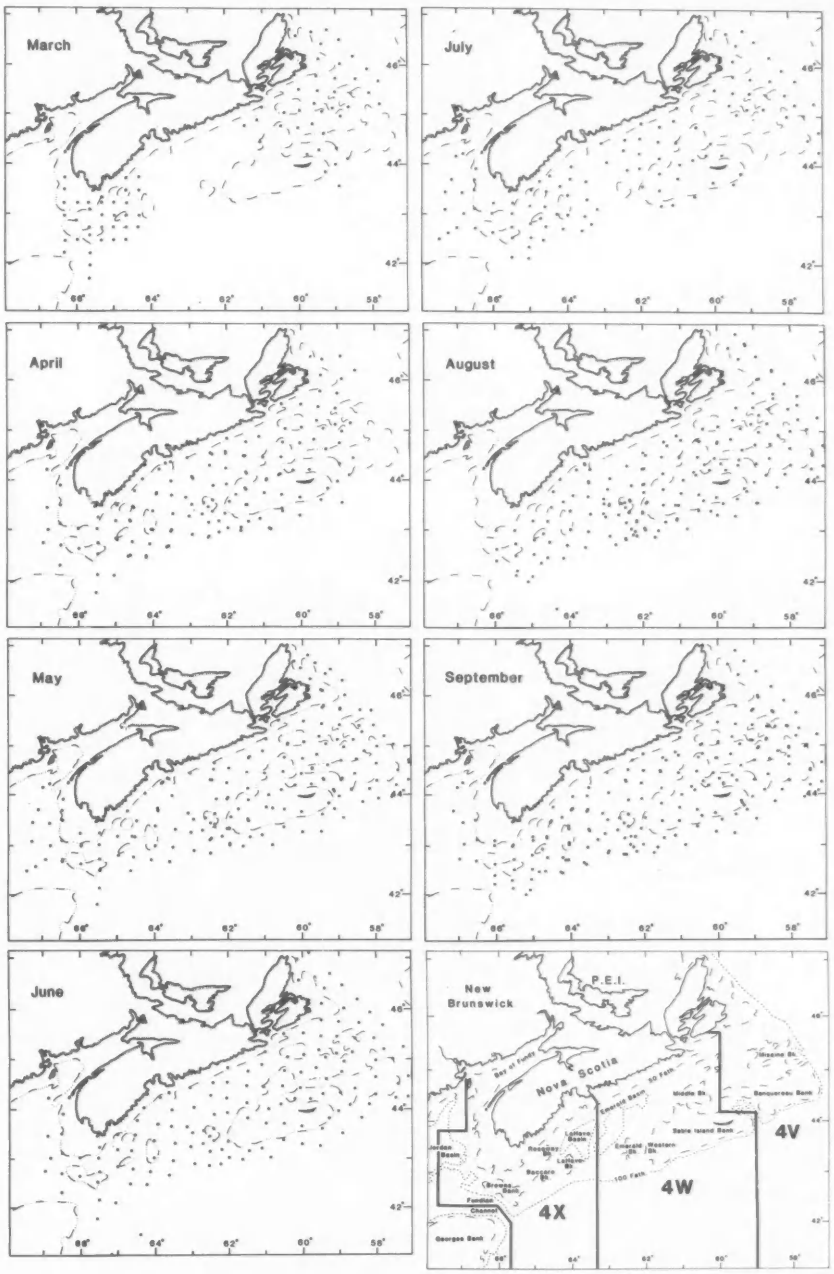

FIG. 1. Stations occupied during the Scotian Shelf Ichthyoplankton Program (1978–82), shown by month from March to September. Bottom right panel shows the locations of hydrographic features referred to in the text and the North Atlantic Fisheries Organization Division boundaries.

delineation of spawning areas is particularly significant, as a genetic basis for division of stocks requires a clear separation of spawning fish, even if they mix at other stages of their life history. Means by which spawning areas can be determined include surveys of mature fish and their reproductive products, leading to information on their spatial and temporal distribution.

From 1978 to 1982, the Scotian Shelf Ichthyoplankton Program (SSIP) conducted by the Department of Fisheries and Oceans provided such data for eggs and larvae on the Scotian Shelf. In this paper, we used SSIP data on egg distributions and timing of appearance of maximum egg densities to examine the stock structure of three commercially important flatfish: Amer-

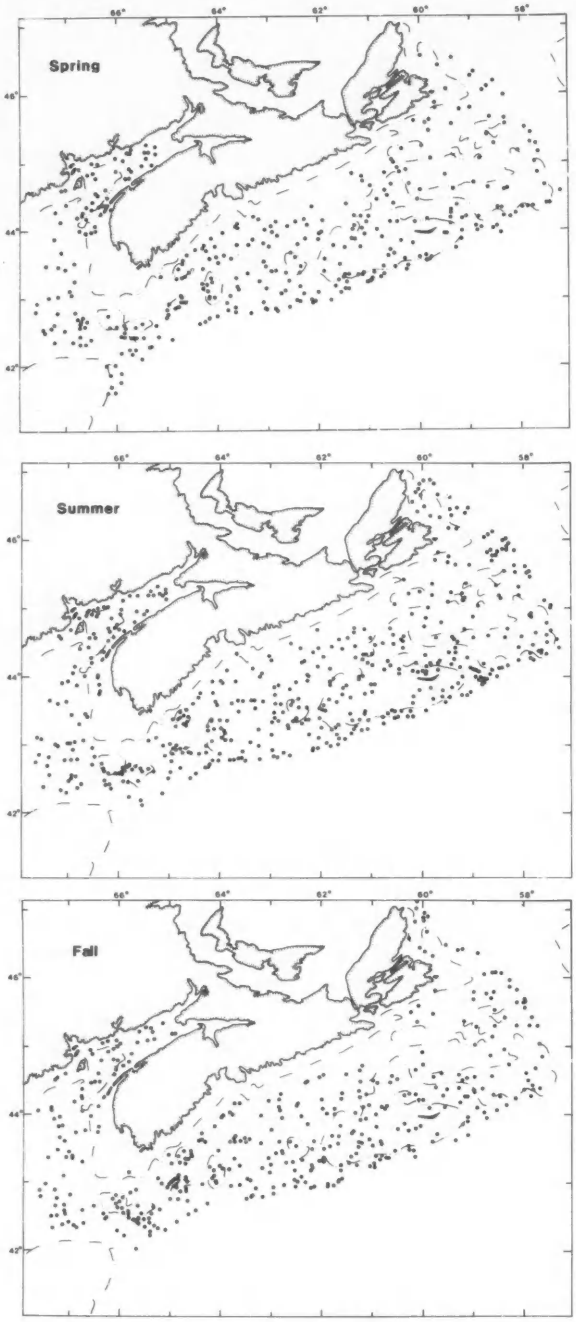

FIG. 2. Stations occupied in random depth-stratified bottom trawl surveys of the Scotian Shelf conducted from 1978 to 1982 each March, July, and October.

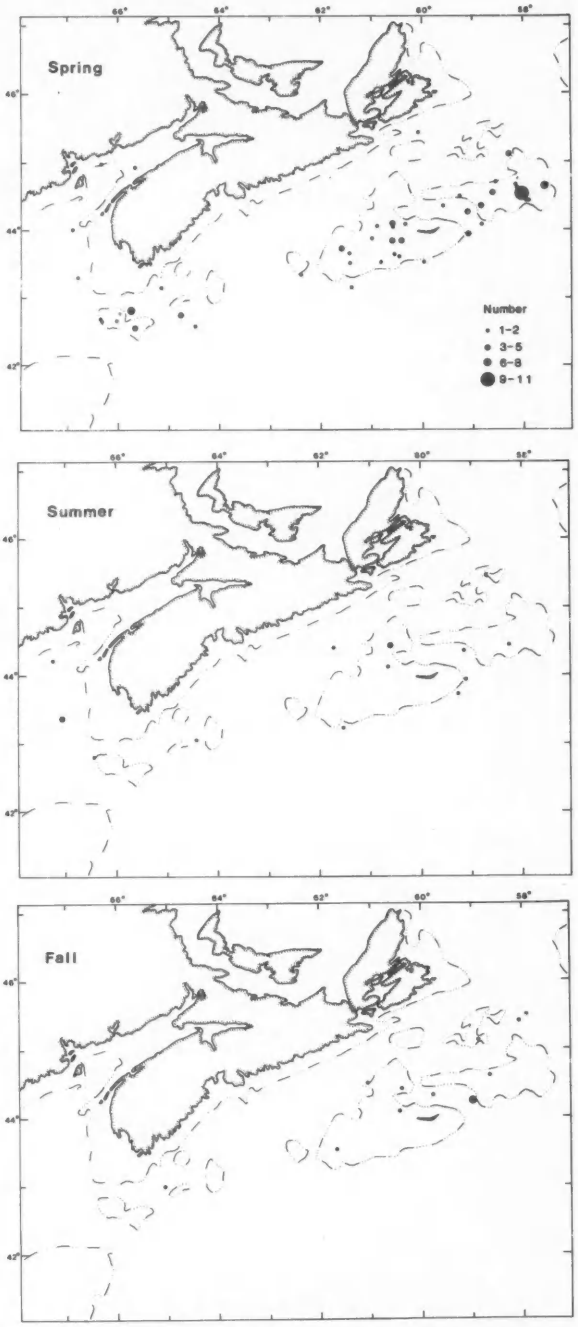

FIG. 3. Distributions of mature American plaice females caught in random depth-stratified bottom trawl surveys conducted from 1978 to 1982 each March, July, and October.

ican plaice (*Hippoglossoides platessoides*), yellowtail flounder (*Limanda ferruginea*), and witch flounder (*Glyptocephalus cynoglossus*). To corroborate our inferences concerning stock structure obtained from examination of the SSIP data, we also examined the distribution of sexually mature adult fish, captured during bottom trawl surveys of the Scotian Shelf, again conducted by the Department of Fisheries and Oceans.

At present, the American plaice fishery in the North Atlantic Fisheries Organization (NAFO) Division 4V (Fig. 1) is considered separately from the rest of the Scotian Shelf (Divisions

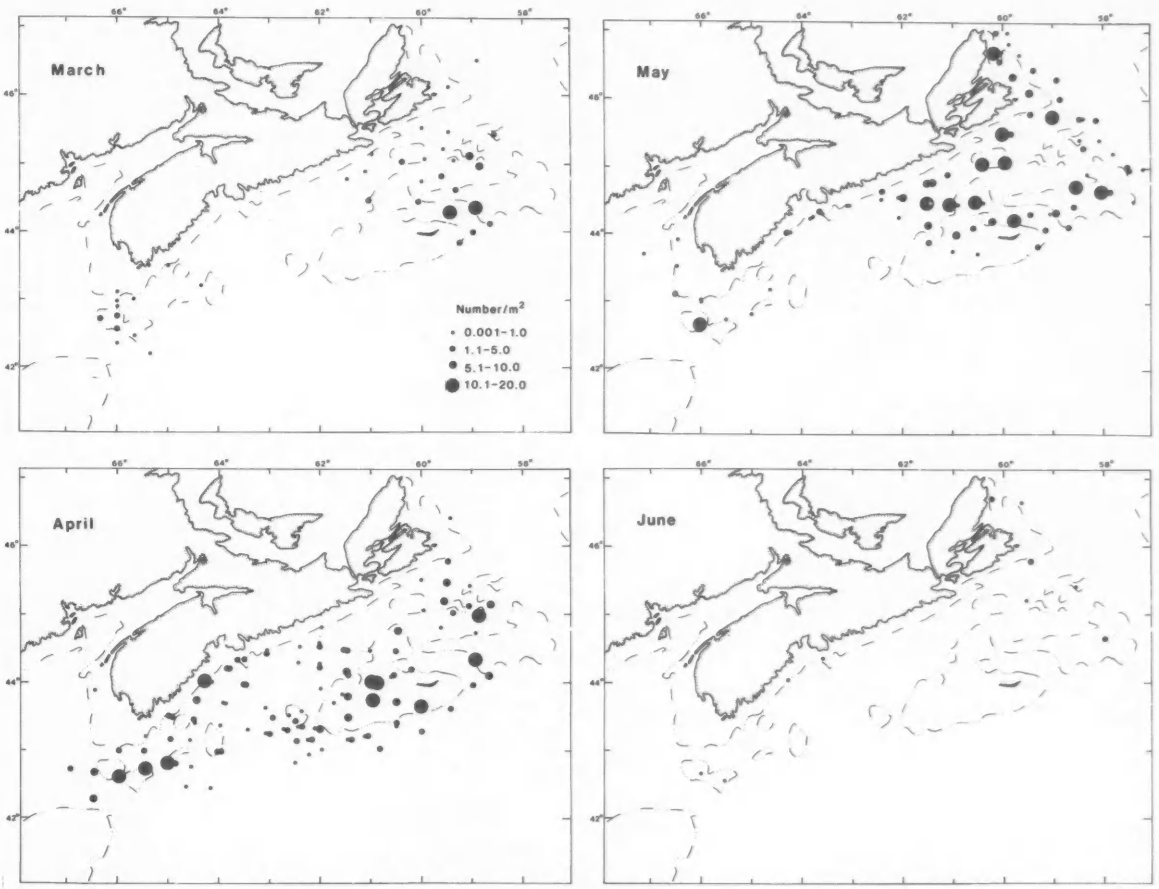

FIG. 4. Distributions of American plaice eggs caught during the Scotian Shelf Ichthyoplankton Program (1978–82), shown by month from March to June.

4W and 4X) for purposes of data aggregation during annual stock size assessments. The witch flounder fishery in Divisions 4V and 4W is considered a single stock whereas yellowtail flounder are managed as a Shelf-wide stock (Neilson and Perley 1986). The geographic limits of the postulated stocks were determined from examinaton of the distribution of the fishery. The data presented here allowed us to examine in more detail whether such aggregations adequately reflect stock structure. While the sampling scale of the SSIP is comparatively coarse for such investigations, the initial hypotheses we suggest will likely lead to more precise studies and a more refined understanding of flatfish stock structure in the future.

While ichthyoplankton data have been used to better define herring (*Clupea harengus*) stock characteristics (Iles and Sinclair 1982), this work is among the first applications of such data to a stock identification study of groundfish in the Northwest Atlantic. Other studies which have used ichthyoplankton data were more limited in scope and addressed problems of stock definition of flatfish of the Gulf of Maine area (Neilson and Hurley 1986; Neilson et al. 1986). In addition to using the SSIP data to examine the adequacy of existing management units with regard to flatfish stock structure on the Scotian Shelf, we review the utility of ichthyoplankton studies for stock identification compared with more commonly employed techniques.

Methods

The survey design for the SSIP program was systematic in nature, with cruises following a standard sampling grid of 150 stations, with approximately 30 km between adjacent stations. Due to logistical constraints, the program concentrated on the portion of the Scotian Shelf beyond the inshore 100-m contour, with only a few stations located near the coast or on the smaller offshore banks. Oblique tows were made with paired 61-cm-diameter bongo nets, each equipped with General Oceanics flowmeters and 333-μm mesh. The nets were lowered to 200 m or to the depth 5 m off bottom (whichever value was less) at a vessel speed of 2.0–2.5 kn, maintaining a 45° wire angle. The rate at which the bongo nets were set and retrieved was 20 and 50m/min, respectively. Plankton samples were preserved in 5% buffered Formalin.

In the laboratory, fish eggs were removed from preserved samples. When the number of eggs in the samples did not exceed 200, all eggs were identified and the development stages determined. In cases where the number of eggs in the sample

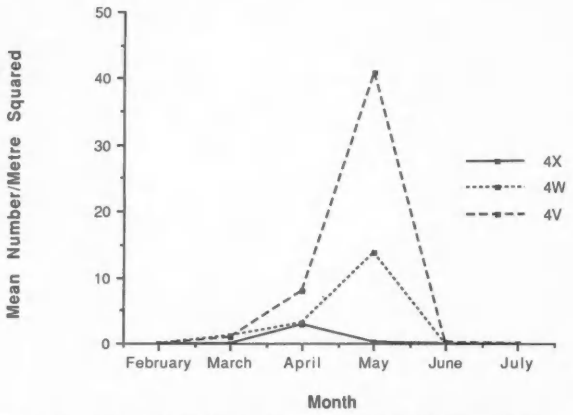

FIG. 5. American plaice egg concentrations (arithmetic means) versus time for North Atlantic Fisheries Organization Divisions 4V, 4W, and 4X, Scotian Shelf, 1978–82.

was greater than 200, the sample was split to create subsamples of 100–200 eggs.

Following the methods described by Markle and Frost (1985), four egg stages were defined: stage 1, from spawning until the visible formation of an embryonic axis about the mid-gastrula; stage 2, from the formation of an embryonic axis until the embryo is halfway around the yolk; stage 3, from the end of stage 2 until the tip of the tail reaches or could reach the snout; stage 4, from the end of stage 3 until hatching. It was often necessary to limit the identification to artificial groupings such as cod/haddock/witch and cunner/yellowtail flounder for stages 1 through 3. Because of such ambiguities in the identification of early stages of witch and yellowtail flounder eggs, only data for stage 4 eggs were used. However, the identification of American plaice eggs is well-established even at the earliest stages of development, so all stages are reported for that species. To assess how well the distribution of late-stage eggs reflected the site of spawning, we also examined the distribution of eggs of American plaice by stage for certain cruises which had adequate geographic coverage and numbers caught.

Abundance was calculated as follows:

$$N_i = C_i F_i D_i / V_i$$

where N_i is egg number per square metre at station i, C_i is the number of eggs counted, F_i is the aliquot multiplier (equal to the number of times the sample was split), D_i is the maximum tow depth (metres), and V_i is the volume filtered (cubic metres).

Insufficient data were available to allow an analysis of egg distribution by year, although subjective examination of the distributions of eggs by year gave us reason to believe that no substantial interannual variability was present. Hence, results from 1979 to 1982 SSIP cruises were combined, providing generally adequate monthly coverage in all months except March. In that instance, data from a 1983 cruise were included. The supplementary information was included for American plaice only, as the March coverage was of no consequence to the other species which spawn later than does American plaice. However, even with the inclusion of the 1983 data, a portion of the Scotian Shelf between Sable Island and LaHave Bank was not covered. A further exception to the generally satisfactory geographic coverage was the relatively deep water area between LaHave and Emerald basins where the station density was comparatively low (Fig. 1).

Egg distributions and concentrations were examined with reference to NAFO Divisions 4X, 4W, and 4V (Fig. 1). Average monthly concentrations (number per square metre) were calculated as the arithmetic mean. As both temporal and spatials trends existed in the data, no reliable estimates of sample variance were possible (Milne 1959).

The data on the occurrence and distribution of sexually mature female flatfish were obtained from regularly scheduled bottom trawl surveys occurring in March, July, and October of each year from 1978 to 1982. The gear employed during such surveys was the Western IIA bottom trawl, equipped with rollers. Sets were 30 min in duration, and towing speed was 3.5 kn. Station locations (Fig. 2) were selected according to a depth-stratified random sampling design (Halliday and Koeller 1981).

Upon haul-back, the fish were sorted by species into baskets. If a large catch of any species occurred, a random subsample of fish was selected for detailed biological observations, including maturity stage, by 1-cm intervals. The maturity stages were assigned for female flatfish as follows:

Stage 1 (immature): ovaries small and firm; pale pink or reddish and somewhat transparent; eggs invisible to the naked eye.

Stage 2 (ripening 1): ovaries slightly larger than in stage 1 but still small and firm; contents microscopic, yellow or reddish yellow, opaque eggs; blood capillaries showing.

Stage 3 (ripening 2): ovaries occupy about half of the ventral cavity; reddish with numerous blood vessels; opaque eggs now visible to the naked eye and give the ovaries a granular appearance.

Stage 4 (ripe): has a few clear eggs at the earliest stage progressing to having mainly clear eggs but eggs do not extrude freely with slight pressure; spawning has not started.

Stage 5 (spawning): as in stage 4, but eggs running freely on slight pressure.

Stage 6 (spent): ovaries soft, flabby, and bloody; partically no eggs remain; purple in colour.

Stage 7 (recovering): membrane purplish and ovaries fairly baggy; no eggs visible.

Stage 8 (resting): looks very much like stage 1, but is found in large fish; ovary larger than in stage 1; also, membrane thicker and not as transparent as in stage 1.

For the purpose of this study, we defined sexually mature fish as those at maturity stages 3–6 inclusively. Data were plotted as numbers of fish per standard tow, where the standard tow length was 1.75 nautical miles at 3.5 kn.

Results

American Plaice

The distribution of mature female American plaice showed some association with the banks of the Scotian Shelf, particularly Browns Bank, Western Bank, and Banquereau Bank (Fig. 3). Fish were also collected a some stations in deeper water, but typically, catches were smaller and infrequent compared with sets made on the banks. The distribution of mature fish was continuous from Banquereau Bank to the southwest as far as Western Bank, with a break around Emerald Basin. Eggs of American plaice were found generally throughout the Shelf with some indication of a discontinuity in the vicinity of Emerald Basin (Fig. 4). The timing of peak reproductive activity appears to differ, with the greatest

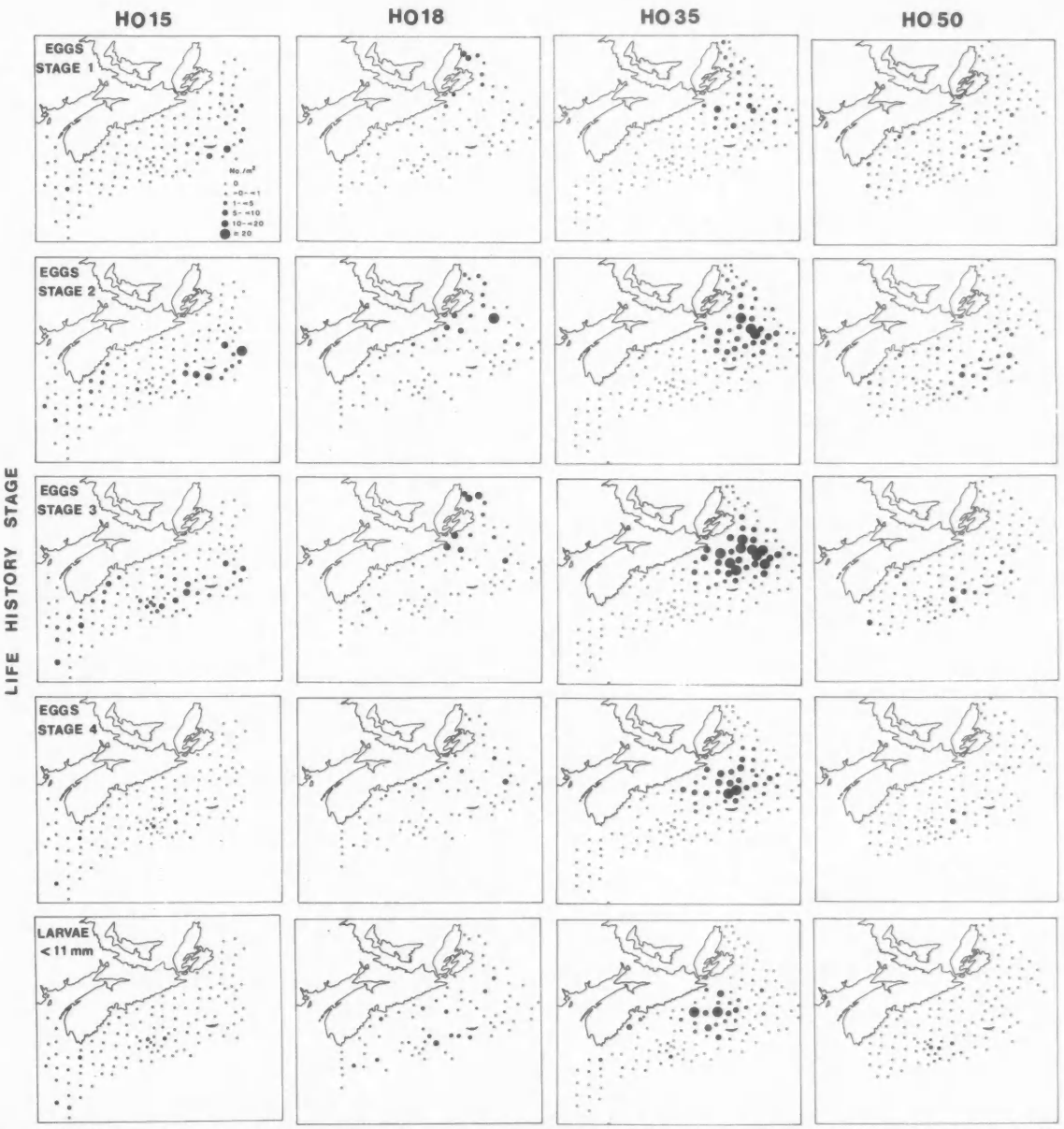

FIG. 6. Distribution of American plaice eggs (by stage) and larvae less than 11 mm from selected cruises on the Scotian Shelf. Cruise HO15 occurred in April 1979, HO18 in May 1979, HO35 in May 1980, and HO50 in March–April 1981.

concentrations of eggs found in April in 4X but in May in 4W and 4V (Fig. 5).

To examine the role of ocean circulation in advection of eggs from spawning grounds, we examined the distribution of plaice eggs (stages 1–4) and larvae from several cruises which had adequate coverage and numbers caught (Fig. 6). Typically, later stages of development showed little or no expansion of the horizontal distribution, at least with the spatial scale of our sampling grid.

Witch Flounder

Of the relatively few mature witch flounder caught during the bottom trawl surveys, most were collected in the vicinity of Western, Sable Island, and Banquereau banks (Fig. 7). The distribution of witch eggs indicated associations with Emerald and Browns banks in May and June, with concentrations of eggs on the more northerly banks (Sable Island, Banquereau) apparent later in the year, around August and September (Fig. 8). Many of the larger catches of witch eggs were associated with relatively deep water off the slopes of the banks, below the 100-m contour. However, some catches of witch flounder eggs were comparatively close to the inshore region in the vicinity of the boundary between 4X and 4W, again near the 100-m

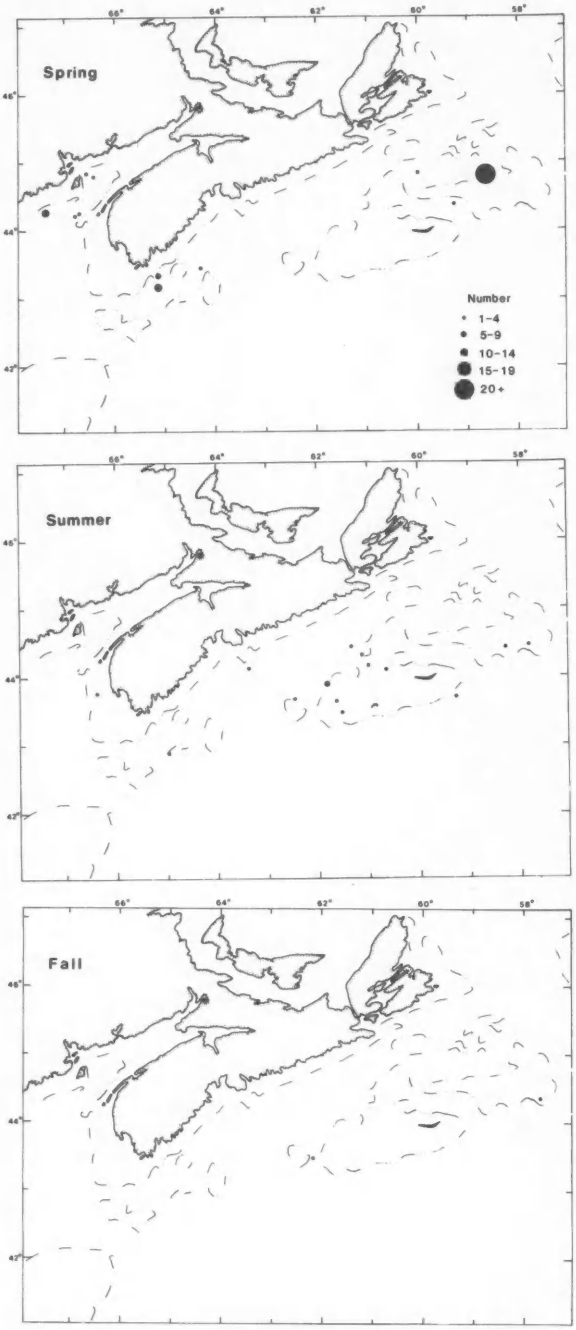

FIG. 7. Distributions of mature witch flounder females caught in random depth-stratified bottom trawl surveys conducted from 1978 to 1982 each March, July, and October.

contour. The plots of egg density versus time (Fig. 9) also reflect a progressive cline in reproductive activity, with 4X peak densities occurring in June, whereas 4V peak densities occurred in August.

Yellowtail Flounder

Of the distributions of mature fish examined, that of yellowtail flounder showed the greatest affinity with the banks of the Scotian Shelf (Fig. 10). Mature fish were present during the spring surveys on Browns, Sable Island/Western, and Banquereau banks. The distribution of mature yellowtail flounder appeared discontinuous between Banquereau and Sable Island banks. The distribution of yellowtail flounder eggs (Fig. 11) also indicated an association with the banks, with concentrations apparent on Browns, Sable Island/Western, and Banquereau banks. However, there were some catches of yellowtail flounder eggs inshore around the 100-m contour. The timing of peak reproductive activity again appeared to follow a north–south cline, with maximum concentrations of eggs in May in 4X and in August in 4V (Fig. 12).

Discussion

Our data indicate that the current method of aggregating data for American plaice stock assessment purposes, were NAFO Division 4V is treated separately from the rest of the Shelf, may be inappropriate. All available data (Fig. 3–5) support the view that two discrete stocks are present: one in NAFO Divisions 4V and 4W and the other in Division 4X. In contrast with our conclusion, O'Boyle et al. (1984) stated that American plaice eggs and larvae were generally distributed over the Shelf. However, the data and analyses presented in that paper (also based on the SSIP surveys) comprised only part of the information now available with the completion of the SSIP and were qualified as being a preliminary interpretation.

Our data (Fig. 7–9) do not allow us to make unequivocal statements concerning witch flounder stock structure. However, given that the eggs and larvae are pelagic (Lange and Lux 1978), with the larval pelagic stage particularly lengthy (up to 1 yr (Markle 1975)), the possibility of interchange among various spawning groups seems considerable. Correspondingly, the probability of correctly identifying discrete unit stocks of witch flounder using such data on the Scotian Shelf is low. Moreover, the utility of the SSIP collections for inferences of stock structure for witch flounder may be problematic, due to the limited depth range sampled. Witch flounder eggs are known to occur in water considerably deeper than 200 m (Evseenko and Nevinsky 1975); thus, it is possible that concentrations of eggs were not adequately sampled during the SSIP program, a view supported by the comparatively low mean densities of eggs obtained in the surveys (Fig. 9). A further aspect of the egg distributions which remains unresolved is the occurrence of catches relatively far inshore in June (Fig. 8). Given that we found that witch flounder spawning activity occurred offshore in comparatively deep water, the occurrence of eggs inshore in June was unexpected. Whether the occurrence of eggs reflected spawning activity in areas not normally covered by the groundfish surveys, or their transport from a more offshore spawning group by an advective process, is not clear. However, Evseenko and Nevinsky (1975) also found eggs relatively far inshore on the Scotian Shelf.

The present means of aggregating yellowtail flounder data for stock assessment purposes is also likely suboptimal. The available data (Fig. 10–12) indicate an even more complex stock structure than was the case for American plaice, with the possibility of separate stocks on Browns, Sable Island/Western, and Banquereau banks. The possibility of separate stocks is

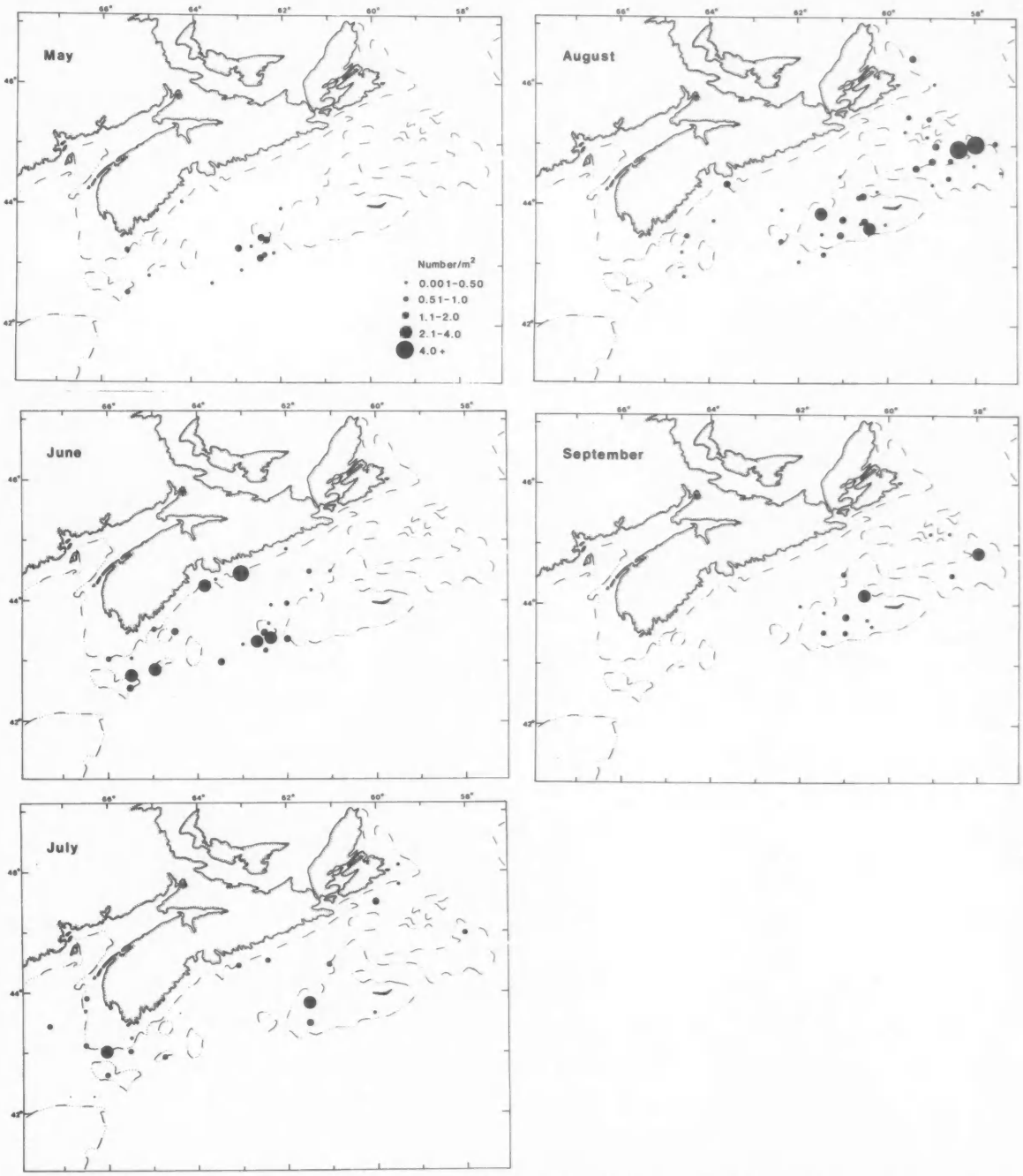

FIG. 8. Distributions of witch flounder eggs caught during the Scotian Shelf Icthyoplankton Program (1978–82), shown by month from May to September.

corroborated by other studies which indicated that yellowtail flounder undertake limited migrations, typically less than 80 km (Royce et al. 1959; Lux 1963; Neilson et al. 1986), and that significant differences in meristic or morphometric features occur in adjacent populations in the Northwest Atlantic (Lux 1963). However, Scott's (1954) study indicated no difference in yellowtail flounder populations located in Middle Bank and Western Bank based on size at sexual maturity, age and size composition, otolith growth, relative growth of three body parts, and a variety of meristic features. As our collections

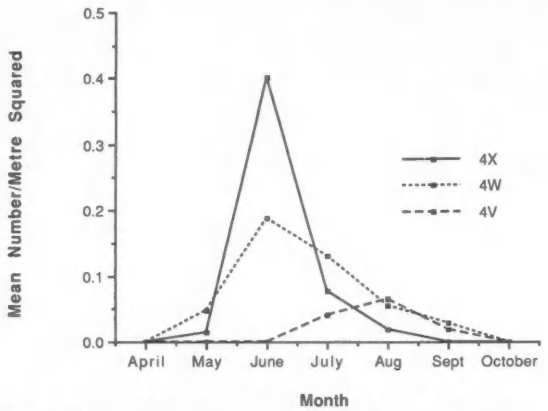

FIG. 9. Witch flounder egg concentrations (arithmetic means) versus time for North Atlantic Fisheries Organization Divisions 4V, 4W, and 4X, Scotian Shelf, 1978–82.

included few yellowtail flounder from Middle Bank, we can neither support nor refute Scott's view. A study of the association of adult groundfish to bottom type indicated that yellowtail flounder were virtually restricted to shallow, sandy substrates (Scott 1982), thereby seemingly further restricting the scope for migration and dispersion, at least at the adult life history stage.

To assess how well the distribution of late stage eggs reflects the site of spawning, it is necessary to consider the period over which eggs were at liberty after release from the female parent. The time from spawning to hatching is 7 d at 10°C in American plaice (Doran 1967), 7–8 d at 7.8–9.4°C in witch flounder (Bigelow and Schroeder 1953), and 5 d at 10–11°C in yellowtail flounder (Hildebrand and Schroeder 1928). Given an average residual current of about 2 cm/s on the Scotian Shelf (Drinkwater et al. 1979), the maximum distance which pelagic eggs are likely to be transported prior to hatching is just under 14 km. While such a calculation is undoubtedly an oversimplification due to aspects such as variation in residual current speed over the depth range in which eggs occur, we nonetheless conclude that the distribution of eggs closely reflects the location of spawning sites for the flatfish species studied here. The view that limited advection of the early life history stages of flatfish occurs on the Scotian Shelf is further supported by Fig. 6.

A feature in common with both the yellowtail flounder and American plaice egg distributions was a discontinuity in the vicinity of Emerald Basin (Fig. 4, 11). We suggest that the discontinuity reflects current patterns on the Scotian Shelf. The general southwest drift along the Nova Scotia coast with a northeast or easterly drift over the edge of the Shelf is believed to create a series of eddies which can at times develop into diffuse gyres (Bumpus and Lauzier 1965). Moreover, analyses of long-term changes in sea surface temperatures indicate that the whole of the Scotian Shelf does not fit into a single regime. The western part of the Shelf displays similar trends in sea surface temperatures as do the Bay of Fundy, the Gulf of Maine, and Georges Bank and may be part of a "southern regime." Similarly, the eastern Scotian Shelf and Grand Banks may be part of a "northern regime" (Trites 1982). We postulate that the concentrations of yellowtail flounder and American plaice eggs observed in this study are consistent with Trites' divison of the Scotian Shelf. The more contiguous distributon of witch

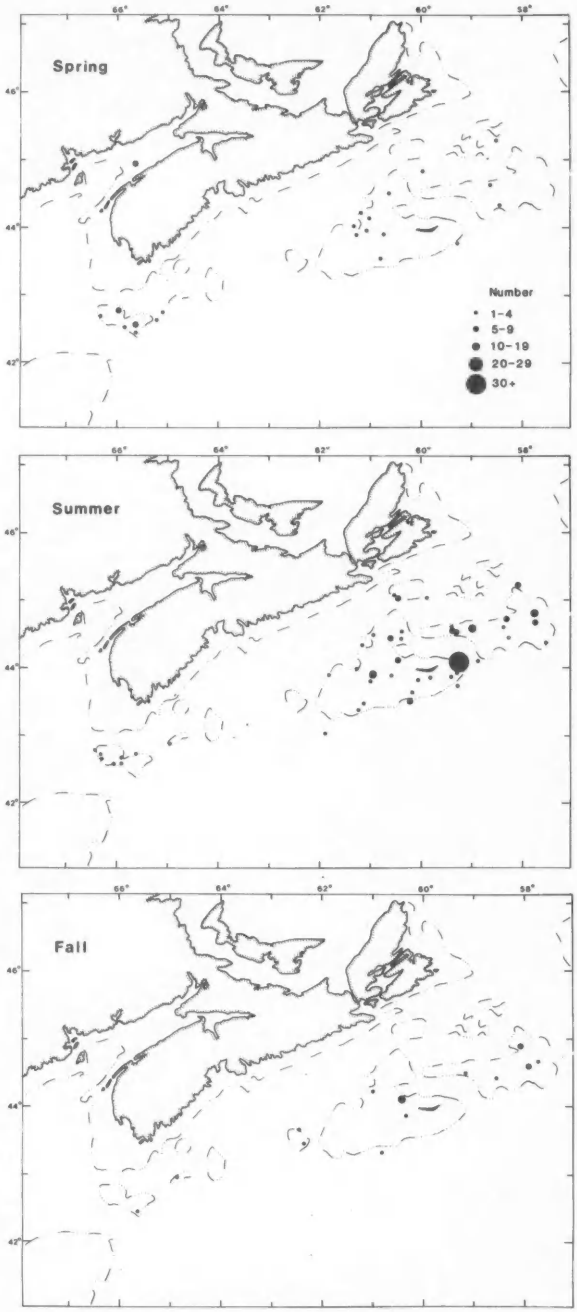

FIG. 10. Distributions of mature yellowtail flounder females caught in random depth-stratified bottom trawl surveys conducted from 1978 to 1982 each March, July, and October.

flounder eggs, on the other hand, appears less consistent with the north and south division of the Scotian Shelf. It may be that the unusual spawning habits of witch flounder, including their preference for deeper water, lead to their reproductive products being more dispersed than those of other flatfish species.

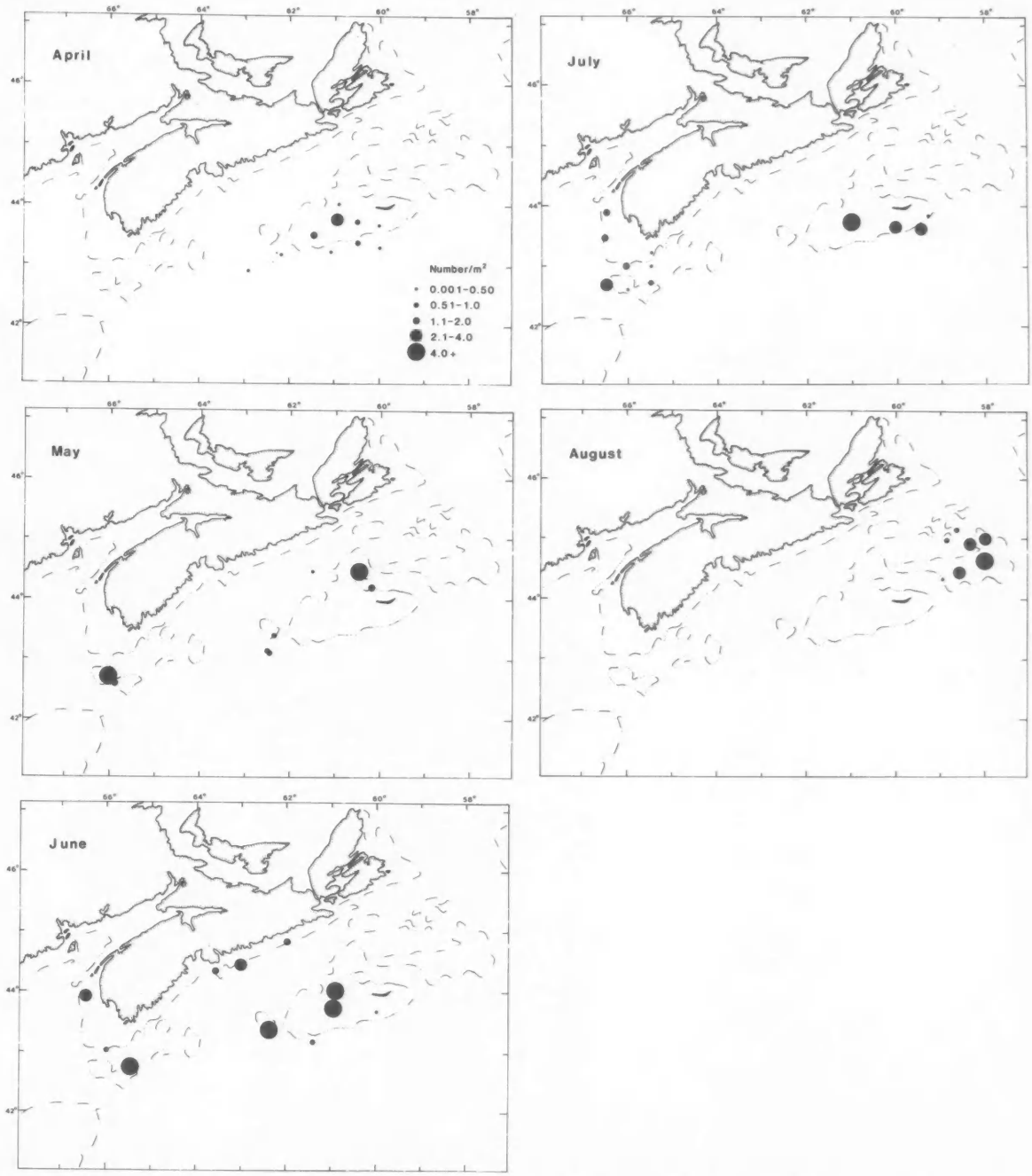

FIG. 11. Distributions of yellowtail flounder eggs caught during the Scotian Shelf Ichthyoplankton Program (1978–82), shown by month from April to August.

The north–south cline in peak reproductive activity apparent for the three flatfish species examined here (Fig. 5, 9, 12) has also been documented for Scotian Shelf cod (Gagné and O'Boyle 1984). In that instance, the spawning of cod appears to take place throughout the fall, ceases in winter, possibly in response to declining water temperature, and resumes in the spring. The cline in reproductive activity evident in this case was that the resumption of spawning activity occurred later with increasing latitude.

A further aspect of the distributional data which may be of

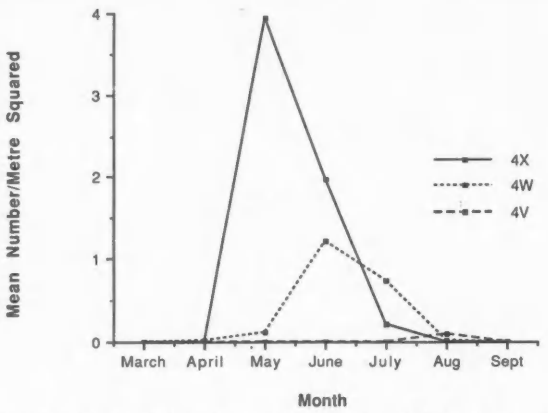

FIG. 12. Yellowtail flounder egg concentrations (arithmetic means) versus time for North Atlantic Fisheries Organization Divisions 4V, 4W, and 4X, Scotian Shelf, 1978–82.

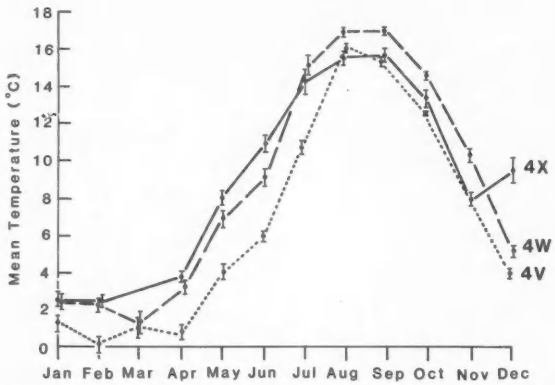

FIG. 13. Mean monthly sea surface temperatures for North Atlantic Fisheries Organization Divisions 4V, 4W, and 4X, Scotian Shelf, 1978–82. Data originate from Scotian Shelf Ichthoplankton Program cruises.

consequence is the close correspondance between distributions of spawning fish and their reproductive products, particularly for American plaice and yellowtail flounder. This observation is in accordance with the view of Iles and Sinclair (1982) who suggested that for herring, the number of genetically distinct stocks is determined by the work of distinct, hydrographically stable larval retention areas. O'Boyle et al. (1984) and Gagné and O'Boyle (1984) also noted that for many species of fish occurring on the Scotian Shelf, both the eggs and larvae appear to be retained over the banks for considerable periods. As pointed out by those authors and further exemplified in this study (Fig. 6), Scotian Shelf fish populations do not seem to follow the pattern of larval drift away from spawning grounds, as suggested by Harden Jones (1968).

However, Koeller et al. (1986) noted on the basis of their examination of the distribution of larvae and juvenile silver hake (*Merluccius bilinearis*) on the Scotian Shelf that larval drift did occur. The apparent discrepancy between their results and those reported here may be attributable to different time of spawning. Silver hake spawn later than the flatfish species, with their spawning period extending from July through October (O'Boyle et al. 1984). It may be that oceanographic conditions during that period were less conducive toward the formation of larval retention areas. Koeller et al. (1986) also followed development of silver hake through a considerably longer period than we were able to, as no collections of postmetamorphosis juvenile flatfish are available.

The cost of obtaining ichthyoplankton data in support of stock identification studies is considerable. For example, the SSIP results reported here are the compilation of data from 25 cruises of approximately 2-wk duration each. Given the cost of vessel charter and provision of adequate manpower both for collection and subsequent sorting and identification, the efficiency of broad-scale larval surveys for stock identification may be questionable. On the other hand, broad-scale surveys, including the SSIP, often have several objectives. Apart from the utility of the data for purposes such as stock identification, they also provide a database which may be of significance for many studies not envisaged at the program inception. In some instances, it may also be that the utility of ichthyoplankton data for stock identification purposes exceeds that of other, more traditional techniques. For example, problems associated with analyses of morphometric and meristic data for stock discrimination include the lack of demonstrable relationships between observed phenotypic variations and the genome of the populations in question (Clayton 1981). Moreover, there are documented effects of environmental variables such as temperature on morphological and meristic features (see Ihssen et al. 1981 for a review). In our case, environmental factors could also be of significance, as it could be argued that the latitudinal clines in peak reproductive activity (Fig. 5, 9, 12) are solely a consequence of higher average water temperature with decreasing latitude (Fig. 13). However, it seems likely that other factors, possibly intrinsic in nature, are of greater consequence. If temperature were the sole factor governing time of reproduction, peaks in reproductive activity would be expected to occur at the same temperature in all three regions. However, we found that peak spawning activity generally occurred at higher temperatures with increasing latitude. Such differences could reflect local adaptions to the environment, which are expected characteristics of discrete stocks.

Acknowledgments

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Reduced Genetic Variability in First-Generation Hatchery Populations of Atlantic Salmon (*Salmo salar*)

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Verspoor, E. 1988. Reduced genetic variability in first-generation hatchery populations of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 45: 1686–1690.

Levels of genetic variation were measured in first-generation Atlantic salmon (*Salmo salar*) cultured for stock enhancement programs in eastern Canada and compared with variation in wild stocks. One regulatory and 19 structural protein loci were screened of which 10 were polymorphic. Mean heterozygosity and number of alleles per locus were positively correlated with the effective number of adults (*N*) used to establish the hatchery groups and averaged 26 and 12% lower, respectively, than wild stocks. The observations are consistent with a loss of genetic variability in the hatchery salmon from random drift caused by using small numbers of salmon for broodstock.

Des taux de variation génétique ont été mesurés chez les individus de la première génération de saumon de l'Atlantique (*Salmo salar*) élevés dans le cadre des programmes de mise en valeur établis dans l'est du Canada, et comparés à la variation relevée chez les stocks de saumons sauvages. On a relevé un locus de régulation et 19 loci de protéine structurale dont 10 étaient polymorphes. L'hétérozygosité moyenne et le nombre d'allèles par locus présentaient une corrélation positive avec le nombre réel d'adultes (*N*) utilisés pour établir les groupes d'écloserie et ces valeurs étaient en moyenne de 26 et de 12 % inférieures, respectivement à celles des stocks sauvages. Les observations sont conformes à une perte de la variabilité génétique chez les saumons d'écloserie provenant de la dérive aléatoire en raison du petit nombre de saumons utilisés comme géniteurs.

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Loss of genetic variability in hatchery fish will generally result in a loss of adaptive potential and, where they are released into the wild, could result in detrimental impacts on the wild stocks (Frankel and Soulé 1981; Allendorf and Ryman 1987). Reduced variability can result from genetic drift, promoted by the use of small numbers of breeders to establish or perpetuate the hatchery groups, or directional selection in the culture environment against specific alleles. Studies of protein variation in Atlantic salmon (*Salmo salar*) cultured in hatcheries for many generations have shown reductions in variability (Cross and King 1983; Ståhl 1983; Vuorinen 1982) and assume the cause to be genetic drift. Levels of genetic variability in first-generation hatchery Atlantic salmon are compared here with levels in wild fish, and the relationship between the level of genetic protein variability and effective numbers of breeders used to establish hatchery groups is examined to assess the importance of drift in any differences.

Materials and Methods

One- and 2-yr-old Atlantic salmon smolts were sampled from 11 hatchery groups established for stock enhancement programs by the Department of Fisheries and Oceans (Canada) derived from salmon taken from nine rivers in New Brunswick and Nova Scotia in eastern Canada (Fig. 1; Table 2). Samples of wild parr and smolts were obtained from seven rivers (Fig. 1; Table 2). The salmon were frozen at approximately −20°C and samples of liver and muscle were removed for electrophoresis.

One regulatory and 19 structural protein loci (Table 1), including three pairs of duplicated loci, Aat-1,2, Gpi-1,2, and Mdh-3,4, were selected for screening on the basis of known polymorphisms (Beland 1979; Cross and Ward 1980; Ståhl 1981 1983, 1987; Claytor 1984) or because they could be conveniently examined at the same time. Samples of muscle and liver, homogenized in an equal volume of 0.01 M 2-mercaptoethanol, were subject to electrophoresis in 11% starch gels at 30 V/cm and 4–8°C for 3–4 h using two buffer systems (Table 1). The stains used are described in Harris and Hopkinson (1976) and, except for SDH and AAT, utilized agar overlays. Ck bands were initially identified using the enzyme-specific stain but otherwise using a bromophenol blue (1% in 4:4:1 methanol–water–acetic acid) general protein stain.

The enzyme nomenclature follows Allendorf and Utter (1979). The designation of loci is that of Johnson (1984) and of the 100 allele follows Cross and Ward (1980) and Ståhl (1987). The PGM regulatory locus is homologous to the diallelic polymorphism reported for rainbow trout (*Salmo gairdneri*) (Allendorf et al. 1982; Johnson 1984; E. Verspoor and C. D. Moyes, unpubl. data). Allele frequencies for this locus were determined from the square root of the frequency of the homozygote for the allele for no expression (*a*), as the two genotypes that result in expression of the PGM locus cannot be reliably distinguished.

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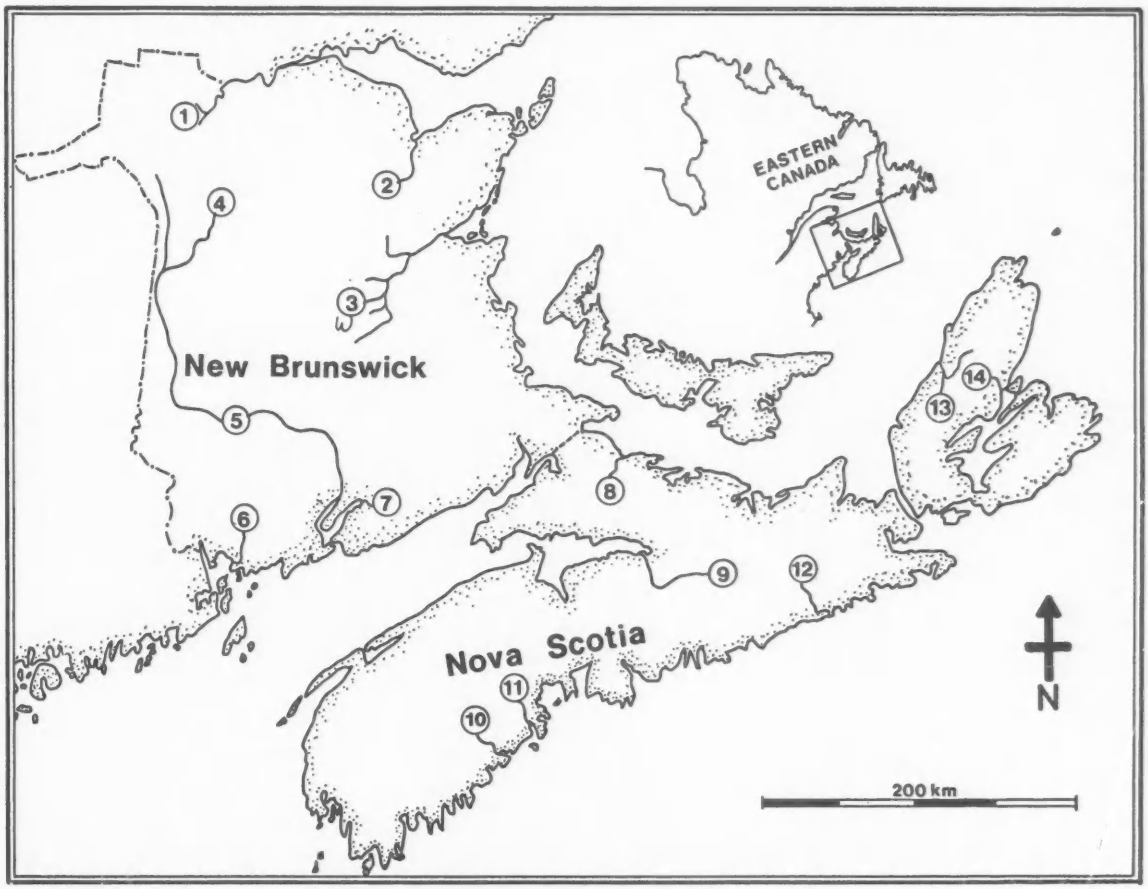

FIG. 1. Location of rivers in eastern Canada referred to in Table 1.

Levels of variability were measured in terms of H, the mean heterozygosity per locus calculated from allele frequencies, and A, the mean number of alleles per locus. Hatchery fish were compared with the wild salmon using the seven hatchery groups derived from salmon in the same, or the geographically nearest, river stocks from which the seven wild samples were obtained. This design minimized differences between the two groups of samples caused by any regional differences in stock allele frequencies. The effective number of salmon used as broodstock from each hatchery groups was calculated using Wright's (1931) N_e which accounts for different numbers of males (N_m and females (N_f) where $N_e = (4N_mN_f)/(N_m+N_f)$. Deviations of genotype proportions from Castle–Hardy–Weinberg were quantified using F_{IS} (Wright 1931) where F_{IS} = (1 − observed/expected heterozygotes). Statistical tests employed are described in Sokal and Rohlf (1981). All G tests incorporate Williams correction, and where multiple tests were involved, significance levels were adjusted to take this into account (Cooper 1968).

Results

Ten loci were polymorphic, having frequencies of the most common electrophoretic allele of 0.99 or less in at least one sample (Tables 1 and 2). Polymorphism at the duplicated locus pairs was in all cases consistent with single locus variation. Only Ck-1 had more than two alleles. Ck-1 (87) occurred in two samples and has been previously reported (Beland 1979), while Ck-1 (65), the only Ck variant in the Hammond River sample, is new. The Hammond River sample also showed a new polymorphism for the Gpi-3 locus involving a (110) allele. Seven samples were variable for a new polymorphism involving the Aat-1,2 duplicated locus pair and a (70) allele.

Two significant heterozygote excesses were detected at the Mdh-3,4 locus, both in hatchery samples (Philip: $F_{IS} = -0.481$, $G = 15.88$, $p < 0.001$; Medway: $F_{IS} = -0.379$, $G = 21.11$, $p < 0.001$). The other loci were not testable. Collectively, both hatchery and wild samples (Table 2) showed among-sample heterogeneity of allele frequencies for most loci. The 1984 and 1985 Bartholemew River samples were pooled, as they were not significantly different at any locus. Neither were the two Nepisiquit River hatchery samples, one derived from early-run and one from late-run fish, significantly different.

The mean heterozygosity per locus, H (Table 2), of the seven selected hatchery samples (0.107) was significantly lower (Mann–Whitney U test, $U = 7$, $p = 0.013$) than among those from the wild (0.145). The mean number of alleles per locus,

TABLE 1. Protein loci screened and their electrophoretic alleles.

Locus	Enzyme (E.C. No.)	Tissue[a]	Buffer system[b]	Alleles[c]
Ldh-4	Lactate dehydrogenase (1.1.1.27)	L	I	100
Pgm-1	Phosphoglucomutase (5.4.2.2)	L, M	I, II	−100
Pgm-2		L, M	I, II	−100
Gpi-1,2	Glucose phosphate isomerase (5.3.1.9)	M	I	100
Gpi-3		M	I	100, 110
Ck-1	Creatine kinase (2.7.3.2)	M	I	100, 87, 65
Ck-2		M	I	100
Sdh-1	Sorbitol dehydrogenase (1.1.1.14)	L	I	100, −72
Sdh-2		L	I	100
Sod	Superoxide dismutase (1.15.1.1)	L	I	100
Mdh-1	Malate dehydrogenase (1.1.1.37)	L	II	100, −50
Mdh-2		L	II	100
Mdh-3,4		M	II	100, 120
Aat-1,2	Aspartate aminotransferase (2.6.1.1)	M	II	100, 70
Aat-3		L	II	100, 50
Me-2	Malic enzyme (1.1.1.40)	M	II	100, 125
Idh-4	Isocitrate dehydrogenase (1.1.1.42)	L	II	100, 116
Pgm1-t	Regulates expression of the PGM-1	L	I, II	*a*, *b*

[a]L = liver, M = muscle.
[b]I = Ridgway et al. (1970) modified by using KOH in place of LiOH; II = Clayton and Tretiak (1972) but at pH 6.6.
[c]Designations based on relative mobilities.

A (Table 2), was also lower (1.5 versus 1.7), but not significantly so (Mann–Whitney *U* test, $U = 14.5$, $p < 0.10$). However, for significantly more loci (7 versus 1), more hatchery samples were monomorphic than were wild samples; for two loci the number monomorphic was the same in the two sample groups (one-tailed sign test, $p < 0.035$). The mean allele frequencies of the seven hatchery samples and the wild samples were not different (Table 2), but allele frequency variation (Table 2) was significantly greater among the hatchery samples for one locus, Pgm1-t (variance ratio test, $F = 14.3$, $p < 0.05$).

H and *A* both show positive correlations with the effective number of adults (N_e) used as broodstock (Fig. 2) when data for all 11 hatchery samples are considered, although only that for *A*, allele number, is significant. At the same time, *H* and *A* are strongly correlated ($r = 0.735$, $p = 0.01$). The association of *H* and *A* with N_e is even more apparent when the effect of sample size (N_s) is taken into account. The partial correlation coefficient for *H* and N_e, holding the effect of N_s constant, is 0.568 ($p = 0.087$) and between *A* and N_e is 0.797 ($p = 0.006$).

Discussion

The hatchery groups of Atlantic salmon examined have 26% less genetic variability, as measured in terms of mean heterozygosity per locus (*H*), than comparable wild stocks. While the lower mean number of alleles per locus is not significant, several considerations suggest that the lower level is real. Firstly, for significantly more loci, more hatchery groups appeared monomorphic than did wild stocks. Also, the hatchery samples used in the comparison averaged 50% larger than those from the wild, introducing a bias in favor of detecting alleles in the hatchery groups compared with the wild stocks. Thus the difference in *A* is probably underestimated. Finally, the strong correlation between alleles per locus and N_e (Fig. 2) supports their being a loss of alleles in the hatchery groups with lower N_e values. The average loss of alleles suggested by the hatchery–wild comparison is 12%.

The positive association of mean heterozygosity and allele number per locus with broodstock numbers points to the lower genetic variability being caused by genetic drift in some of the groups. There is also an indication of an increased allele frequency variance among the hatchery samples and an absence of differences in mean allele frequencies between the two sample groups, consistent with drift. Mean allele frequencies might be expected to differ if selection for or against alleles had occurred. Furthermore, hatchery samples from the Restigouche and the Saint John rivers ($N_e > 45$) show little or no reductions in variability compared with wild samples from the same rivers, as is predicted by theoretical considerations of drift. Theory suggests that most (>99%) genetic variability will be preserved if N_e of the broodstock is >50 (Denniston 1978; Frankel and Soulé 1981; Allendorf and Ryman 1987).

Previous studies of genetic variability in hatchery fish have examined levels of variability in fish that have been maintained by culture for at least several generations (Allendorf and Ryman 1987). The findings of the present study show, as theory predicts, that losses in genetic variability can occur even in the first hatchery generation if numbers of fish used for broodstock are not sufficient. Indeed, the average reductions in variability detected here are of the same order as those observed in other Atlantic salmon maintained by hatcheries for a number of generations. Cross and King (1983) found the levels of heterozygosity and numbers of alleles to be 27 and 12.5% lower in salmon artificially maintained for five generations by a sea ranching operation, while Ståhl (1983) found levels of heterozygosity to be 20% lower in Swedish hatchery salmon.

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TABLE 2. Allele frequency data. Letters indicate hatchery and wild samples used in comparison of two sets of

Map No.	River of origin	N_e	N_s	Pgm1-t (*a*)	Gpi-3 (100)	Ck-1 (100)	Sdh-1 (100)	Mdh-1 (100)	Mdh (10
									Locus/allel
							Hatchery samples		
1A	Restigouche	46.7	70	0.169	1.0	1.0	0.036	0.914	0.8
2B	Nepisiquit L	16.0	100	0.332	1.0	1.0	0.010	0.965	0.8
	Nepisiquit E	12.4	50	0.245	1.0	1.0	0.010	1.0	0.7
5	Saint John H	50.9	70	0.462	1.0	1.0	0.029	0.921	0.8
C	Saint John W	14.4	100	0.480	1.0	1.0	0.050	0.955	0.8
8D	Philip	14.7	65	0	1.0	1.0	0	1.0	0.5
9E	Steviake	14.7	49	0.247	1.0	0.929	0	1.0	0.8
10F	Medway	2.7	100	0.728	1.0	1.0	0	1.0	0.6
12	Liscombe	6.4	45	0.298	1.0	1.0	0	1.0	0.3
13G	Margaree	6.0	100	0.374	1.0	1.0	0	1.0	0.9
14	North	6.0	25	0	1.0	1.0		1.0	0.5
Mean (A–G)			83.4	0.333	1.0	0.990	0.014	0.976	0.7
Variance (A–G)				0.054	—	0.001	<0.001	0.001	0.0
Heterogeneity (all samples)[b]				111.2***	—	29.2*	34.4**	70.0***	182.3
							Wild samples		
1A	Restigouche		30	0.365	1.0	1.0	0	1.0	0.8
3B	Bartholemew		98	0.335	1.0	1.0	0.015	0.980	0.7
	1984		68	0.364	1.0	1.0	0.015	0.985	0.7
	1985		30	0.258	1.0	1.0	0.017	0.967	0.7
4C	Saint John		62	0.524	1.0	1.0	0.032	0.911	0.8
6D	Maguagadavic		58	0.394	1.0	1.0	0.034	0.957	0.7
7E	Hammond		42	0.345	0.810	0.988[c]	0.214	0.952	0.8
11F	LaHave		53	0.532	1.0	0.991	0	0.972	0.5
13G	Margaree		44	0.374	1.0	1.0	0.035	0.989	0.7
Mean			55.3	0.410	0.973	0.997	0.047	0.966	0.7
Variance				0.007	0.005	<0.001	0.006	0.001	0.0
Heterogeneity[b]				8.3	67.6***	3.2	49.6***	15.1	34.0

[a]H = mean heterozygosity per locus; A = mean number of alleles per locus.

[b]G test with Williams correction for sample size (Sokal and Rohlf 1981), based on allele count except f frequency was used. Significance levels corrected for multiple comparisons: *$p < 0.025$, **$p < 0.01$, *** p

[c]Stock where variant allele is Ck-1 (65).

o sets of samples.

cus/allele						
Mdh-3,4 (100)	Aat-1,2 (100)	Aat-3 (100)	Me-2 (100)	Idh-4 (100)	H^a	A^a
0.857	0.986	0.036	0.093	1.0	0.102	1.7
0.805	0.990	0.030	0.035	0.915	0.115	1.8
0.790	0.990	0.110	0	0.929	0.107	1.6
0.843	1.0	0.079	0.064	0.936	0.135	1.7
0.875	1.0	0.030	0.080	0.910	0.127	1.7
0.579	0.954	0.100	0.077	0.877	0.111	1.4
0.847	1.0	0	0.020	1.0	0.080	1.4
0.671	1.0	0	0	1.0	0.084	1.2
0.344	1.0	0	0	0.989	0.089	1.3
0.920	0.960	0.180	0.160	0.965	0.132	1.6
0.540	1.0	0	0	0.900	0.067	1.2
0.793	0.984	0.054	0.066	0.952	0.107	1.5
0.015	<0.001	0.004	0.003	0.003		
182.3***	30.7**	102.4***	87.4***	71.7***		
0.817	1.0	0.067	0.167	0.983	0.120	1.5
0.740	0.969	0.148	0.046	0.883	0.151	1.8
0.757	0.037	0.147	0.059	0.875		
0.700	0.017	0.150	0.017	0.900		
0.831	1.0	0.065	0.097	1.0	0.130	1.6
0.793	1.0	0.103	0.121	0.991	0.137	1.7
0.845	1.0	0.298	0.155	0.976	0.220	1.9
0.537	1.0	0	0	0.981	0.110	1.5
0.750	0.965	0.045	0.116	0.886	0.149	1.8
0.759	0.991	0.104	0.100	0.957	0.145	1.7
0.011	<0.001	0.009	0.004	0.003		
34.0***	15.6	57.1***	39.2***	42.9***		

except for Pgm1-t where the *a/a* homozygote
, *** $p < 0.001$.

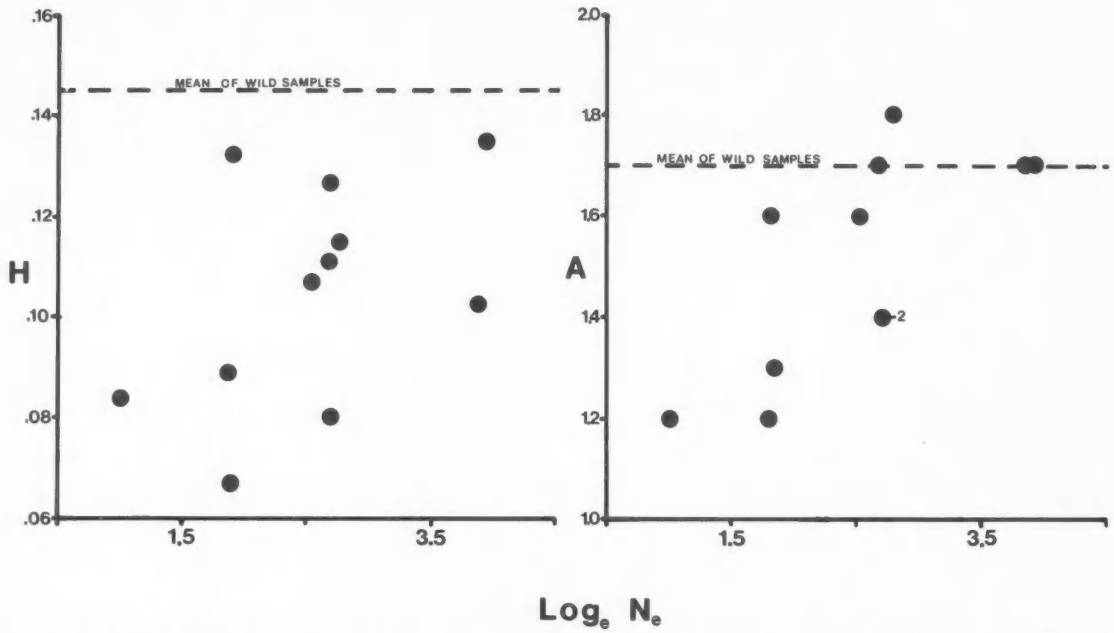

FIG. 2. Mean heterozygosity per locus (H) and alleles per locus (A) plotted against N_e, the effective number of male and female broodstock, for 11 hatchery populations of Atlantic salmon.

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Within-River Spawning Migration of Atlantic Salmon (*Salmo salar*)

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Heggberget, T. G., L. P. Hansen, and T. F. Næsje. 1988. Within-river spawning migration of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 45: 1691–1698.

The migration pattern of adult spawners of Atlantic salmon (*Salmo salar*) in two Norwegian streams was analysed by ultrasonic and mechanical tagging to investigate within-river migration. Salmon were tagged in the estuary as they approached the river before spawning. They displayed a systematic and directional upstream pattern of movement in the river. Seventy-one percent of the fish transplanted 6 km downstream from the capture site about 2 mo before spawning returned to the donor area. Fish transported 7 km upstream from the capture site exhibited a low degree of backtracking to the donor site (one of seven fish). Mechanical tagging of salmon on spawning grounds showed that both male and female spawners released 150 and 600 m upstream from the spawning area were able to return to the original site of spawning with a mean precision of 87%. In both streams, the migration pattern and the return to original site of capture support the hypothesis of local homing of Atlantic salmon, although some fish stray to other areas of the stream.

Le profil de migration des géniteurs adultes de saumon de l'Atlantique (*Salmo salar*) dans deux cours d'eau de la Norvège a été étudié par le marquage aux ultrasons et l'étiquetage mécanique afin d'analyser la migration dans les rivières. Les saumons ont été marqués dans l'estuaire avant leur arrivée dans les frayères. Dans la rivière, ils se déplaçaient suivant un profil général vers l'amont. Soixante et onze pour cent des poissons transplantés 6 km en aval du lieu de capture 2 mo environ avant de frayer sont retournés à leur lieu d'origine. Les poissons transportés 7 km en amont du lieu de capture avaient peu tendance à revenir au lieu d'origine (un poisson sur sept). Le marquage mécanique des saumons dans les frayères a montré que les géniteurs mâles et femelles relâchés 150 m et 600 m en amont de l'aire de frai pouvaient retourner à leur lieu d'origine pour frayer avec une précision moyenne de 87 %. Dans les deux cours d'eau, le profil de migration et le retour au lieu de capture d'origine confirme l'hypothèse selon laquelle le saumon de l'Atlantique revient à son lieu d'origine pour frayer, même si certains poissons se sont dirigés vers d'autres aires du cours d'eau.

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Homing to their natal river is well documented in Atlantic salmon (*Salmo salar*) (Huntsman 1942; Carlin 1968). Donaldson and Allen (1958), Wagner (1969), and Quinn and Fresh (1984) have found that adult Pacific salmon and steelhead trout (*Salmo gairdneri*) not only returned to their native streams, but also to the sites of release within streams. The results from these studies are mainly based on statistical interpretations of release/recapture data obtained by tagging large numbers of fish. These studies give little or no detailed information of riverine behavior or migration patterns of the fish. Knowledge of riverine behavior of adult Atlantic salmon is essential in studies of local homing.

Recent development of advanced telemetry equipment (Gray and Haynes 1979; Westerberg 1982) has made detailed analyses of movements of salmon possible. However, most telemetric studies of salmonid spawning migrations have been limited to specific areas of rivers or areas in estuaries (Johnson 1960; Trefether and Sutherland 1968; Coutant 1969; Monan and Liscom 1976; Gray and Haynes 1977). Couturier et al. (1986) tracked landlocked Atlantic salmon by using acoustical techniques and found that tagged fish mostly returned to initial capture site.

Heggberget et al. (1986) suggested the existence of local populations within the River Altaelva, Norway. Presmolts that lived their first years in the upper section of the river returned to the nursery area after having been at sea. Existence of local homing requires that the salmon are able to relocate the nursery area of a stream when returning as spawners. Little is known about details of the within-river spawning migration of Atlantic salmon. The aim of the present study is to analyse the movements of upstream migrating salmon and fish displaced before and during spawning in two Norwegian streams.

Study Areas

Altaelva

The catchment area of the River Altaelva (70°N, 23°E) is 7400 km^2 and the mean annual waterflow is about 77 m^3/s. Atlantic salmon is the dominant fish species. The average annual catch during the last 10 yr was about 19 000 kg with a mean weight of 8.1 kg for individual salmon. No fish have been introduced during the last 20 yr, and salmon in the river are exploited only by rod fishing. The salmon in the Altaelva mostly comprise grilse (30%) and 3-sea-winter fish (55%). Most (93%) of the grilse are males, while 3-sea-winter fish are predominantly females (80.4%).

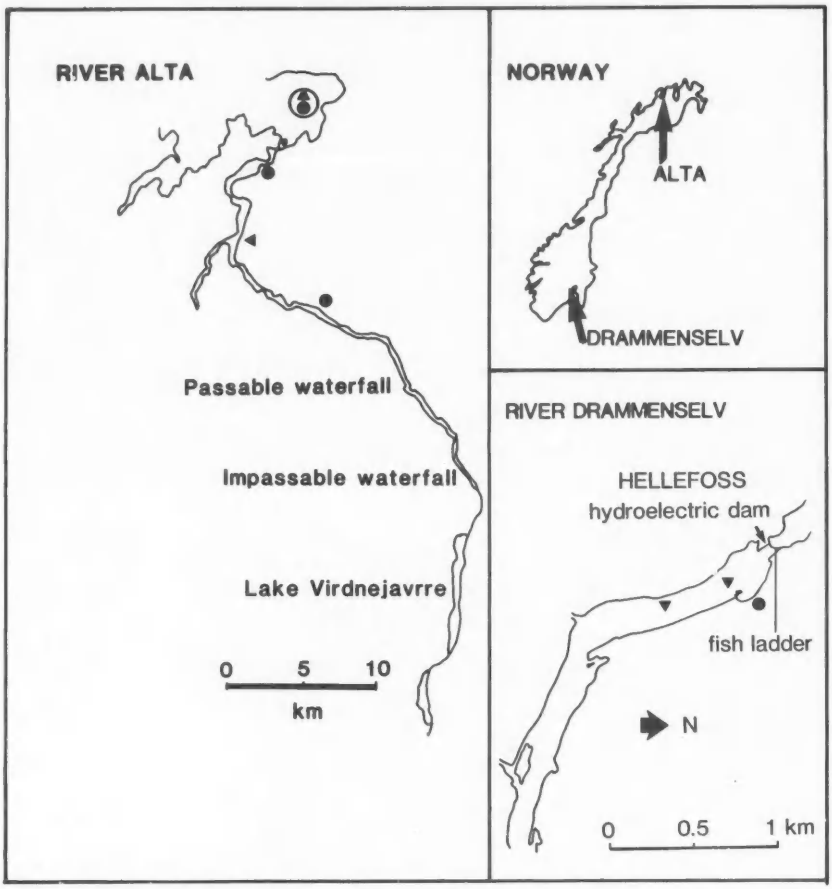

FIG. 1. Rivers Altaelva and Drammenselva showing sites of catch and release of adult salmon. ⊛, of catch and release in the estuary; ▲ capture site; ●, release sites.

The fish used for the experiments were caught at two localities: in the estuary about 5 km outside the river (experiment I) and in the river about 11 km upstream from the outlet (experiment II) (Fig. 1). The tagged fish were released at three different sites both on and off the expected migration route (Fig. 1). No physical barriers for upstream or downstream migrations of fish exist between the releasing points. Salmon spawning areas are well distributed along the 46 km of the river accessible for upstream migrating fish.

Drammenselva

The catchment area of the River Drammenselva (60°N, 10°E) is 17 140 km² with mean annual waterflow of 225 m³/s. In recent years, an enhancement program including release of hatchery-reared fingerlings and smolts of local stock has increased the number of spawners (Hansen et al. 1986). More than 90% of the grilse are males, and about 90% of the 2-sea-winter fish are females. Among 3-sea-winter fish, there are about equal proportions of each sex.

The fish used in the experiments were caught at two closely situated localities (Fig. 1). The waterfall upstream from the release area was impassable for upstream migrating fish.

Materials and Methods

Altaelva

Atlantic salmon enter the Altaelva on their way to the spawning areas mainly between late May and late August, with a peak in the first half of July. Hydroacoustic tagging was performed in the estuary in late June and early July 1985 and in the river in mid-August 1986. In experiment I, fish were caught by bagnets in salt water when they approached the Altaelva. Fish used in experiment II were caught by seine in the river. On the basis of results from experiment I, it was assumed that most of the fish had stopped at their spawning area by that time.

During tagging, the fish were placed in a partially covered cylindrical tank filled with oxygenated water. Without anesthesia the transmitters were attached behind the dorsal fin by two steel wires. After tagging, the fish were kept in oxygenated water for 1–3 h to allow initial recovery before release. The cylindrical (5.5 × 1 cm) transmitters weighed 12 g and each had its own frequency and pulse rate, which allowed the observer to track fish individually. Further description of the transmitters and receivers is given in Mohus and Holand

(1983). The fish were transported in closed tanks of oxygenated water and were not allowed to experience the water between the capture and release sites.

Several factors may affect the results obtained by hydroacoustic tagging of fish. The endurance of the transmitters differed considerably; several ceased transmitting after a relatively short time, limiting the number of fish for analysis. In experiment I, eight fish released in the estuary were tracked for a period of 20–130 d from entering the river until spawning. In the displacement experiments, 14 fish were released 6 km downstream (experiment IIa) and seven fish were released 7 km upstream (experiment IIb) from the original capture site (Fig. 1). The fish were located once to twice each week in the period between release and spawning.

Behavioral effects from handling and tagging fish are difficult to estimate (Hawkins et al. 1974; Westerberg 1983). Negative effects appear to be most pronounced during the first days after release. Therefore, we payed little attention to the migration pattern observed during the first 5 d after release. In our experiments, those transmitters that failed during the first 15 d after release were excluded from the analysis. Based on the low weight and small size of the transmitters compared with the size of the fish, problems associated with buoyancy of the fish (Fried et al. 1976) or with reduced swimming capacity due to external tags (Arnold and Holford 1978; Shepherd 1973; McCleave and Stred 1975) were unlikely.

Drammenselva

In experiment III, performed in 1985 and 1986, a total of 302 salmon were caught with driftnets at Hellefoss (184 females, 118 males) and 126 salmon at Storstein (99 females, 28 males) (Fig. 1). The salmon were tagged with Carlin tags (Carlin 1955) and released about 100 m upstream from Hellefoss (Fig. 1) after 1–2 wk in captivity. The distance between Hellefoss and Storstein is about 500 m. The experiment took place during the spawning period, and both mature and stripped fish were tagged. Systematic fishing with driftnets took place in the two areas 1–4 wk after release.

Results

Altaelva

Experiment I (fish captured and released in the estuary)

The period from release in the estuary to entrance into the river varied from 4 h to 2 wk. Seven of the eight salmon that entered the river were located 1 km upstream from the river's mouth within 72 h after release (Fig. 2). The distance travelled during the first 5 d after entering the river varied between 1 and 14 km, with a mean of 6.2 km. After 5 d in the river, the mean migration distance decreased, and no movements were recorded later than 25 d after entering the river. No downstream movements were recorded. All fish moved upstream until stopping at the locality where they maintained position until spawning (holding position). The mean time from entering the river to establishing a holding position was 14 d (range 5–24 d). The mean distance travelled upstream was 13 km, and the fish stopped in spawning areas in the lower half of the river. No fish remained in the same pool, indicating that no pool was more preferred than others.

Experiment IIa (fish released 6 km downstream from the original site of capture)

Adult salmon released downstream from the original site of capture moved both upstream and downstream (Fig. 3). During the first 5 d, two of the salmon did not move. The rest of the fish (85%) moved a mean distance of 7.3 km. Five of these fish

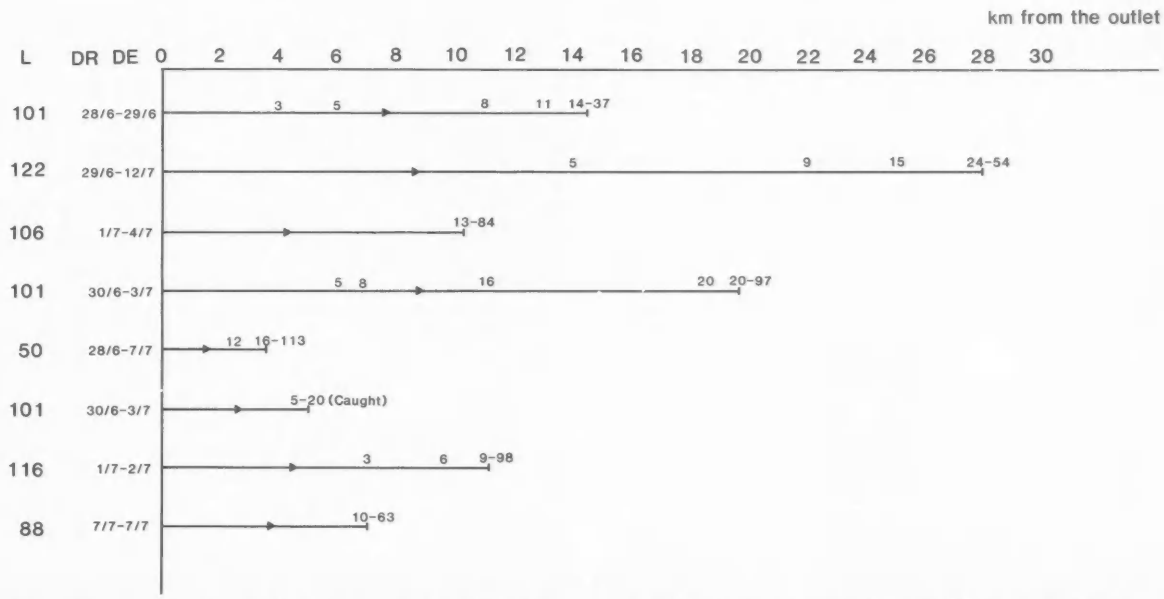

FIG. 2. Movements of salmon in the Altaelva released in the estuary. L = length of fish (cm), DR = date of release, DE = date entering river. Single numbers indicate days after entering the river when leaving a certain area. Double numbers (5–15) indicate days after entering the river when arriving at the holding position (first number) and the number of days observed the last time at that site (last number).

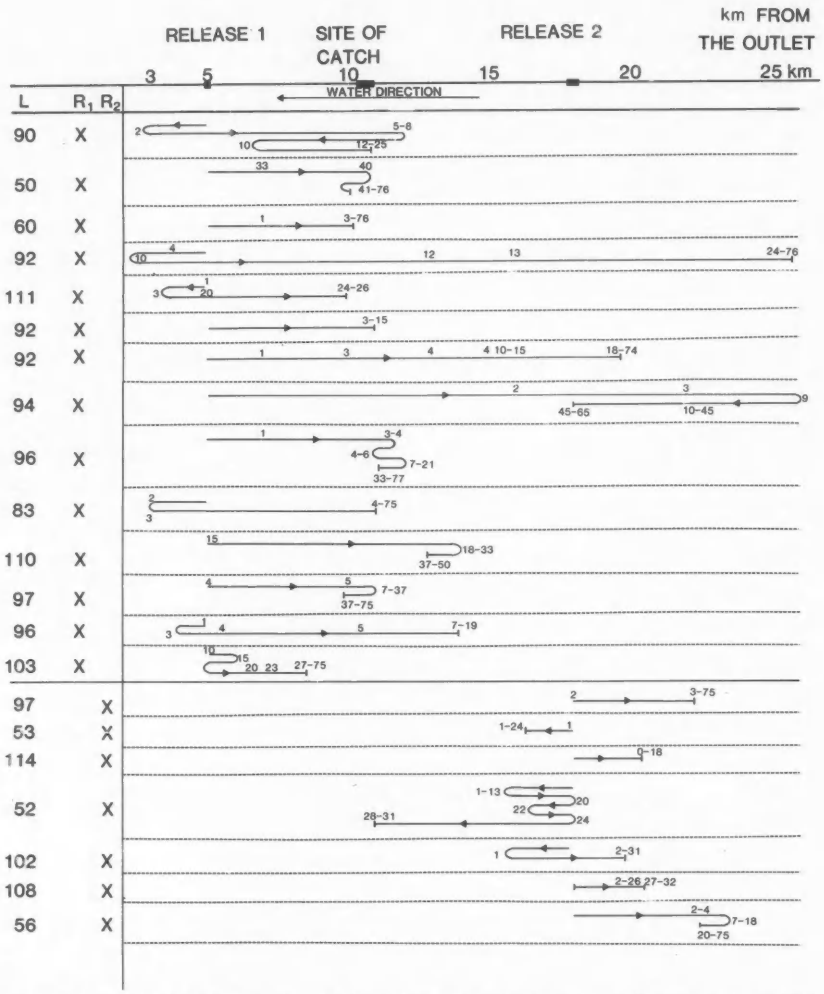

FIG. 3. Movements of displaced salmon in the Altaelva released downstream (R_1) and upstream (R_2) from the site of capture in the Altaelva. Symbols as in caption to Fig. 2.

(42%) moved both upstream and downstream and one fish moved only downstream during this period (Fig. 4).

In the next 5–10 d, the proportion of fish that moved (43%) as well as the overall distance moved decreased (Fig. 4). These six fish moved a mean distance of 3 km during this period. Both upstream and downstream movements occurred.

Changes in the movement patterns of some fish were observed when they reached or passed their original capture area. Five salmon displayed upstream and downstream movements after they reached or passed the area where they were originally captured. Four fish passed the area of original capture without backtracking and migrated a mean distance of 12.5 km further upstream before they stopped. Most of these fish remained there until spawning or failure of the transmitter, while one fish slowly returned downstream during the period 10–65 d after release. This salmon was located about 8 km upstream from the original site of catch at the time of spawning.

Ten (71%) of the fish released downstream returned to and stopped permanently in the area of original capture (±2 km). Eight of the fish (57%) returned to the pool where they were initially caught. The proportion of fish that returned is therefore between 57 and 71%, depending on the definition of the extension of original area of capture (Fig. 5).

Time elapsed from release to return to area of original capture varied between 3 and 37 d, with a mean of 12.5 d. Most of the fish (60%) that returned did so within 3–5 d after release. The mean distance travelled for all fish tagged in experiment IIa was 2.3 km downstream and 9.7 km upstream, or a mean total of 12.0 km. The final distribution of the salmon in experiment IIa shows a mean distance from site of capture of 3.1 km, varying between 0 and 14.7 km. All salmon that established holding positions outside the initial catch area (±2 km) were found upstream of the catch site.

Experiment IIb (fish released 7 km upstream of the original place of capture)

All salmon used in experiments IIa and IIb were caught in the same area. Fish released 7 km upstream from the site of capture moved a mean distance of 3.3 km and displayed both

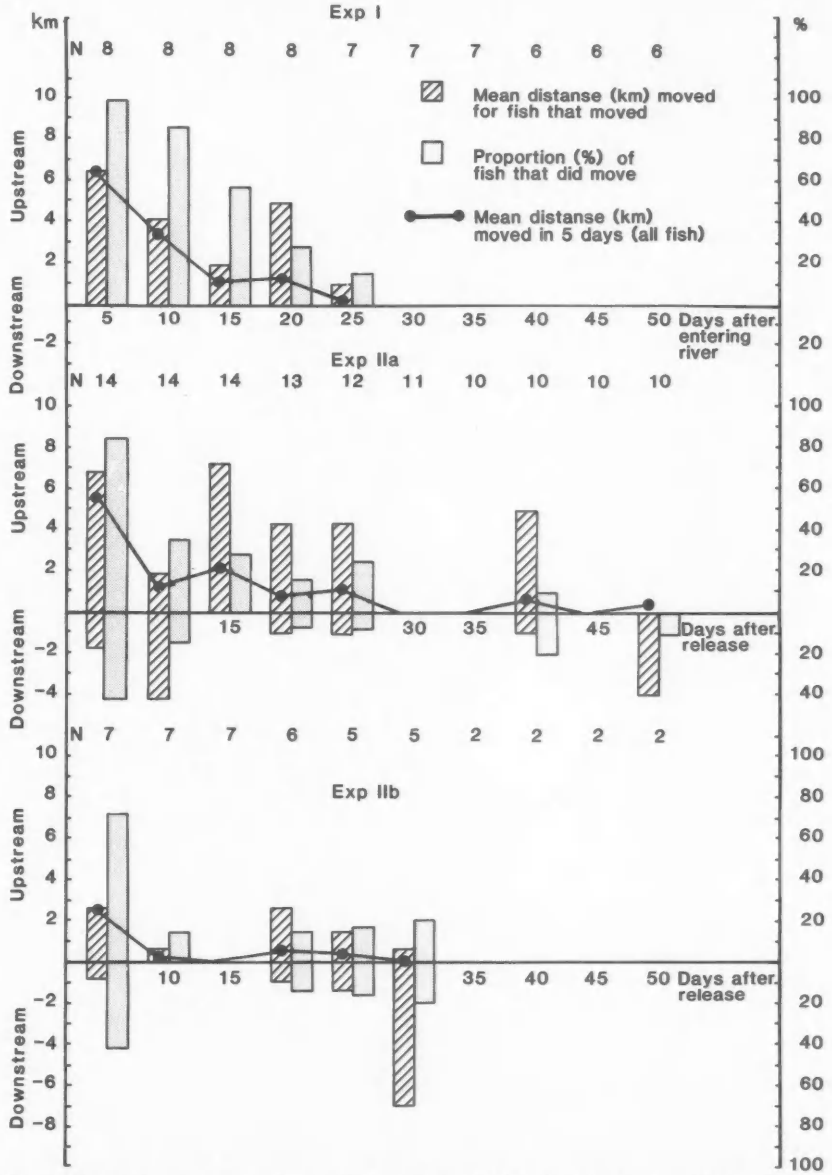
Exp I
km
%
N 8 8 8 8 7 7 7 6 6 6
Mean distanse (km) moved for fish that moved
Proportion (%) of fish that did move
Mean distanse (km) moved in 5 days (all fish)
Upstream
Downstream
5 10 15 20 25 30 35 40 45 50 Days after entering river
Exp IIa
N 14 14 14 13 12 11 10 10 10 10
15 30 35 45 Days after release
N 7 7 7 6 5 5 2 2 2 2
Exp IIb
10 15 35 40 45 50 Days after release

FIG. 4. Mean distances moved and proportion of the tagged fish in the Altaelva moved during the first 50 d after release. Exp. I = salmon tagged and released in the estuary; Exp. IIa = salmon displaced downstream site of catch in the river; Exp. IIb = salmon displaced upstream site of catch in the river.

upstream and downstream movements during the first 5 d after release (Fig. 3). One of the fish moved both upstream and downstream during this period. Three of the salmon moved a mean distance of 0.9 km downstream, while five salmon moved a mean distance of 2.5 km upstream from the site of release.

During the 5–10 d after release, only one fish (14%) moved (1.5 km upstream). During the next 25-d period (10–35 d after release), only two fish moved. The longest distance travelled by a fish involved several upstream and downstream movements in the release area before it backtracked and arrived at the original site of capture 28 d after release (Fig. 3).

Many of the fish in experiment IIb were lost shortly after release (mean 22.8 d). However, in the period when the transmitters were operating, the fish displaced upstream moved shorter distances and less frequently than the fish released downstream.

The fish released downstream had a more clustered distribution around the site of original capture than the fish released upstream (Kolmogorov–Smirnov two-sample test, $P < 0.05$; Sokal and Rohlf 1981). The final distributions of fish (Fig. 5) in the two groups (experiments IIa and IIb) were also significantly different when mean distances from the site of catch were compared. (ANOVA, $P < 0.025$).

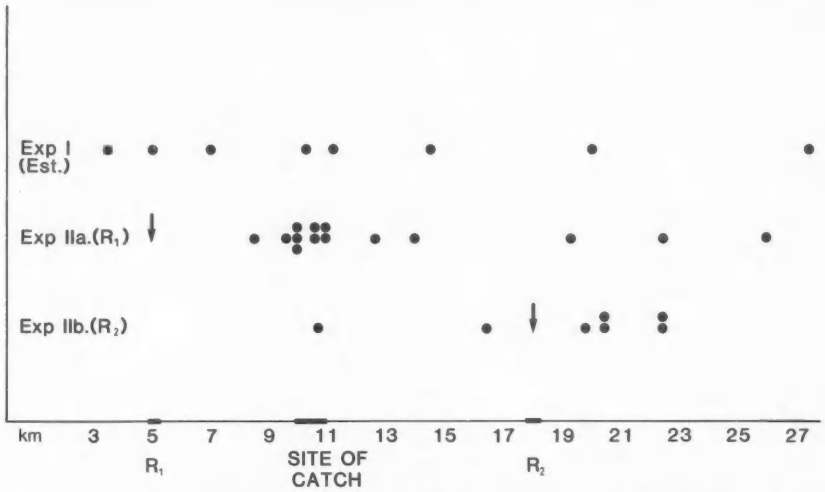

FIG. 5. Final distribution of tagged salmon in the Altaelva. For explanation of the different experiments, see caption to Fig. 4.

TABLE 1. Number of tagged males and females of Atlantic salmon recaptured at two spawning areas, Storstein and Hellefoss, in the River Drammenselva.

Site of original capture		Recaptured at Storstein	Recaptured at Hellefoss
Storstein, 1985	Males	11	4
	Females	0	2
Storstein, 1986	Males	5	0
	Females	0	0
Hellefoss, 1985	Males	3	42
	Females	2	10
Hellefoss, 1986	Males	0	7
	Females	0	1

Drammenselva

Experiment III (fish released 100–600 m from the original capture site during spawning)

Of the 261 salmon released in 1985, 74 fish were recaptured within a month after release (Table 1). The fish caught at the spawning area at Hellefoss returned to Hellefoss with high precision. Some fish caught at Storstein were recaptured at Hellefoss, but the majority were recaptured in the area where they were originally caught. This repeated return was highly significant (G-test, $P < 0.01$), as was also the case in 1986 when all the fish were recaptured in the original spawning area (G-test, $P < 0.01$).

On November 25, 1985, 56 stripped salmon (51 originally from Hellefoss and 5 originally from Storstein) were tagged and released in the estuary about 30 km downstream from the site of capture. Four fish originating at Hellefoss were recaptured at Hellefoss 3–4 d after their release. One fish originating from Storstein was recaptured at Storstein 8 d after release. None were found elsewhere.

Discussion

An important question when interpretating the data from the displacement experiments in the Altaelva is whether or not the salmon involved had established holding positions. If they had not established home areas, a return to areas farther upstream from the capture site would be expected. The downstream displacement showed that some fish migrated farther upstream from the original site of capture. One possible explanation is that these fish were only moving through the area where they were originally captured. The present results (experiment I) indicate that most salmon had established holding positions by the middle of August. However, local informants report upstream migrating salmon also in late August and even in September, about 1 mo before peak spawning (October 15–25).

The pattern of movements found in the Altaelva (experiment I) differs from that of adult hatchery-reared Atlantic salmon released as smolts both in headwaters and at the head of the tide in the Penobscot River, Maine, USA (Power and McCleave 1980). The fish tracked in the Penobscot River moved both upstream and downstream, interspersed with position holding, although they tended to move less towards the time of spawning. A tendency towards homing to a particular tributary was observed. Power and McCleave (1980) suggested that the variable behavior and lack of strong upstream movement of salmon in the Penobscot River may be due to the lack of genetic adaption to the Penobscot River drainage, the scarcity of conspecifics with their possible pheromonal influence, or the lack of a home stream and concomitant motivation to stimulate unimprinted salmon to progress upstream. Another explanation for the different migration patterns observed in the Altaelva and the Penobscot River may be the existence of several dams in the latter that disturbed the upstream migration of salmon. In the Altaelva there are no physical barriers in the area studied.

Atlantic salmon moved rapidly through the estuary and lower reaches of the River Dee, Scotland, before stopping (Hawkins and Smith 1986). Farther upstream, progress was achieved by phases of active swimming interspersed with stationary periods spent in pools. On several occasions, fish were observed to move downstream during exceptionally high water flows. However, the general migration pattern observed in the River Dee is not very different from that of the Altaelva, despite the fact that salmon may enter the River Dee long before spawning.

Our results are similar to two other studies. Helle (1966) carried out comprehensive studies of homing of displaced pink salmon (*Oncorhynchus gorbuscha*) and concluded that 53–73% of the displaced fish returned to their donor site. In a study of prespawning migration of lake-dwelling resident Atlantic salmon in southeastern Newfoundland, Couturier et al. (1986) found that 8 of 10 sonic tagged fish were relocated close to their original capture site within 10 d after release.

Other literature on localized homing by Pacific salmon within a river system, as reviewed by Ricker (1972), has confirmed that salmon tend to drop back in an attempt to find their home areas after artificial displacement upstream or accidental overshooting. Taft and Shapovalov (1938) also reported downstream movements of rainbow trout that had bypassed their homestream spawning site. This kind of behavior connected to overshooting of a formerly established area was also observed in the Altaelva, indicating that the salmon were actively searching for the original capture site.

The failure of upstream displaced salmon to return to the initial catch site is supported by a number of studies with Atlantic and Pacific salmon (e.g. Fish and Hanavan 1948; Helle 1966; McNeil et al. 1969; Ducharme 1972; Farwell and Porter 1976; Kennedy et al. 1977). Contradictory results have been reported by Andrew and Geen (1960). They found that when sockeye salmon (*Oncorhynchus nerka*) were transported to a barren spawning area above an impassable waterfall, they did not spawn there, but returned to downstream areas. In the Drammenselva, there is a waterfall shortly upstream from the site of release, preventing fish from moving further upstream. A major difference from most of the experiments cited is that the salmon in the Drammenselva were released very close to the areas of their original capture.

The results from Drammenselva demonstrate that salmon displaced a short distance upstream are able to reestablish formerly selected spawning areas with high precision. The higher straying to Hellefoss of fish originating from Storstein and released 100 m above Hellefoss might indicate that the precision of repeat homing decreased with increased migrating distance, particularly for fish released above their original site of spawning. By transplanting adult steelhead trout upstream from the site of their original capture, Cramer (1981) found that fish transplanted farther upstream were less likely to move downstream.

Based on the undirectional waterflow and suggestions that olfaction is an important cue for local navigation in salmonids (Hasler and Wisby 1951; Wisby and Hasler 1954; Groves et al. 1968; Hasler et al. 1978; Johnsen and Hasler 1980; Westerberg 1982), a better homing response is expected in downstream displaced fish than in upstream displaced fish.

During the prespawning period, about 70% of the displaced fish in the Altaelva were recovered within 2 km of the site of capture. Given assumed effects of handling and tagging procedures of behavior, and the likelihood that some fish had not yet established holding positions, the straying rate of salmon under natural conditions is probably lower than the 30% nonreturn observed in the Altaelva.

Although the sample was small, some of the fish released in the Drammenselva estuary returned to their spawning areas despite the fact that they had been manually stripped, indicating that the homing behavior remains for some time after stripping. The reason for this may be a defence of the spawning area for some time after spawning.

In general, the systematic directional movements of upstream migrating salmon together with a significant return to donor sites of downstream displaced fish support the hypothesis of homing to specific areas within the river. Return of adult Atlantic salmon to areas of origin in a river has been shown by Power and McCleave (1980). Thompson (1951, cited in Banks 1969) and Hartman and Raleigh (1964) have suggested that different spawning populations of sockeye salmon are maintained by homing to specific tributaries. In addition, there are several examples among Atlantic and Pacific salmonids where different forms of the same species utilize different portions of the same watershed for spawning (Ricker 1938; Dehring et al. 1981; Riddell and Leggett 1981; Ryman and Ståhl 1981; Miller and Brannon 1982).

Even if a system of local homing produces minor or no genetic differences, homing to nursery areas will act as a mechanism to ensure optimal quantitative distribution of spawners in areas of high and low production in a river.

Straying acts as a mechanism to counteract local genetic specialization. Straying also ensures rapid colonization of fish in unstable, low productive areas or damaged areas of a river. A certain amount of straying should be regarded as an alternative to homing. The two behavioral patterns exist in dynamic equilibrium where within-river homing is the main mechanism for evolution of several stocks within a river system.

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Blood Oxygen Capacity Differences in Yellow Perch (*Perca flavescens*) from Northern Wisconsin Lakes Differing in pH

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Nelson, J. A., J. J. Magnuson, and W. Chulakasem. 1988. Blood oxygen capacity differences in yellow perch (*Perca flavescens*) from northern Wisconsin lakes differing in pH. Can. J. Fish. Aquat. Sci. 45: 1699–1704.

Whether chronic exposure to environmental acidity reduces oxygen loading in fish is still uncertain. We evaluated this question by looking for evidence of adaptations to hypoxia in a population of yellow perch (*Perca flavescens*) isolated in a well-oxygenated, naturally acidic lake. Perch were sampled directly from this naturally acidic lake (pH 4.5) and two circumneutral lakes, one of which experiences low oxygen. Fish were bled rapidly via cardiac puncture. Hemoglobin, hematocrit, and erythrocyte number were determined by standard methods. Hemoglobin concentrations were highest in perch from the acid lake (6.4 g/dL) intermediate in the neutral lake with anoxic zones (5.7 g/dL) and lowest in the well-oxygenated neutral lake (4.8 g/dL). Increased hemoglobin per red cell accounted for this trend. Slightly larger hematocrits in acid lake perch (41.2 versus 36.2) were achieved through small increases in red cell number and volume. Evidence suggests that these results are part of an adaptational response different from the hematological responses of fish to acute acid exposure.

Nous ne savons pas encore si une exposition chronique à des conditions environnementales acides réduit la charge en oxygène chez les poissons. Nous avons étudié cette question en cherchant des preuves d'adaptation à des conditions hypoxiques chez une population de perchaudes (*Perca flavescens*) isolées dans un lac naturellement acide et bien oxygéné. Des perchaudes ont été échantillonnées directement à partir de ce lac naturellement acide (pH 4,5) et de deux lacs presque neutres, dont l'un à faible teneur en oxygène. Les poissons ont été saignés rapidement par ponction cardiaque. La mesure de l'hémoglobine et de l'hématocrite et la numération des érythrocytes ont été effectuées par des méthodes courantes. La teneur en hémoglobine était plus élevée chez les perchaudes du lac acide (6,4 g/dL), intermédiaire dans le lac neutre comportant des zones anoxiques (5,7 g/dL) et plus faible dans le lac neutre bien oxygéné (4,8 g/dL). Une teneur accrue en hémoglobine par globule rouge était responsable de cette tendance. On a obtenu des valeurs pour l'hématocrite un peu plus élevées chez les spécimens provenant du lac acide (41,2 contre 36,2) en faisant augmenter légèrement le nombre de globules rouges et le volume. Les données semblent indiquer que ces résultats font partie d'une réaction d'adaptation différente des réactions hématologiques des poissons à une exposition aiguë à des conditions acides.

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Acidification of freshwaters throughout Scandinavia and North America has sparked interest in physiological responses of fish to acidic environments. One topic of concern and controversy has been whether a hydrogen ion induced shift in the hemoglobin-oxygen binding curve reduces oxygen loading in the gills of chronically acid-stressed fish. If low environmental pH reduces the blood pH in the secondary lamellar capillaries, then the oxygen–hemoglobin equilibrium would shift towards deoxyhemoglobin (Bohr effect) and the oxygen carrying capacity of hemoglobin would diminish (Root effect). Experimental tests of this idea in many laboratories have produced equivocal results (see Wood and McDonald (1982) for a review). It is also not clear whether compensatory responses in blood oxygen capacity occur in acid-stressed fish. Furthermore, when investigators have shown increased hematocrit or hemoglobin levels in acid-exposed fish (Dively et al. 1977; Neville 1979a; Vaala and Mitchell 1970), it was unclear whether these responses resulted from hemoconcentration due to acute salt and water loss or were a compensatory response to reduced oxygen loading. Hematological characteristics of rainbow trout (*Salmo gairdneri*) undergoing acute acid stress (pH 4.0–4.5; 3 d) result from a combination of erythrocyte swelling and splenic contraction (Milligan and Wood 1982). There is no strong evidence that sublethal acid stress induces either hypoxemia or compensatory erythropoeisis.

We hypothesized that if oxygen loading is inhibited in fish exposed to low environmental pH, then perch in northern Wisconsin lakes exposed to gradually increasing acidity over the last 10 000 yr would show compensatory responses in their oxygen loading system. Blood variables that help determine blood oxygen capacity such as hemoglobin concentration and erythrocyte number are heterogeneous within a population and generally responsive to environmental conditions (Grigg 1974). We hypothesized that perch in naturally acidic lakes, through natural selection or ontogenetic acclimatization, could increase some of these factors to offset the potential diminution of oxygen loading at the gills. To test this idea, we measured the blood oxygen capacity variables, hemoglobin, hematocrit, and erythrocyte number in freshly captured yellow perch (*Perca flavescens*) from a naturally acidic lake and two circumneutral ref-

TABLE 1. Selected physical and chemical characteristics of the three study lakes. Data for Trout and Allequash Lakes taken from the Northern Lakes University of Wisconsin-Madison chemical data base. Data for Wharton Lake taken from Rahel (1983) and the present study. Winter oxygen profiles were taken during the first week of March 1986 for all three lakes. Values for winter oxygen are at just under the ice, 6 m depth, and 1 m off the bottom.

Lake	Area (ha)	Maximum depth (m)	Mean annual pH	Conductivity (μmho/cm)	Alkalinity (mg $CaCO_3$/L)	Winter oxygen (mg/L)		
						0.5 m	6 m	Bottom
Wharton	13	6	4.4	9	0	8	1.8	0.30
Trout	1566	35	7.6	63	27	11.9	11.4	2.1
Allequash	164	10	7.9	79	39	7.5	1.3	0.11

erence lakes. To our knowledge this is the first comparison of the hematology of feral fish populations from naturally acidic waters with conspecifics from neutral waters.

Materials and Methods

Yellow perch of uniform total length (120–245 mm; mean = 172 mm) were sampled from one naturally acidic and two circumneutral lakes in Vilas Co, Wisconsin (Table 1), four times during July and August 1983. Two additional collections were made in the fall of 1983. Comparable measurements could not be made during winter because of problems with sluggish blood flow and blood freezing. The two reference lakes (Allequash and Trout) are connected by a stream and gene flow is possible between their perch populations. Both lakes were included in this study to understand how the appearance of hypoxic waters in Allequash Lake and not in Trout Lake influenced the measured variables in neutral pH lakes. All fish were captured by angling during daylight hours.

Angling was chosen as the method of capture to minimize capture time and standardize the presampling treatment of the fish. Net capture was excluded because of greater struggling and variable capture times. Electrofishing was not used because of the low conductivity of Wharton Lake (Table 1). No alternative technique enabled us to secure the fish as rapidly with as little struggling. The fish were secured as quickly as possible (~10 s), blotted with absorbent tissue to avoid surface mucus and water contamination (~10 s), and then bled via cardiac puncture into heparinized plastic syringes, except in September 1983 when several fish were bled via the caudal vein. Fish were then weighed and measured and either returned to the lake or frozen. Blood was drawn into heparinized syringes and immediately placed on ice until transported to a field station where the samples were stored at 4°C until assayed. Hematocrit was determined upon return to the field station (average 4.5 h) and hemoglobin was determined within 16 h.

Hematocrit was determined by centrifugation at 3000 × *g* in microhematocrit capillary tubes. Hemoglobin was measured by a cyanomethemoglobin method. Drabkin's reagent and hemoglobin standard were from Sigma Chem. Co. Optical density was recorded at 540 nm in a Beckman DU spectrophotometer. For fish collected in July and August, an aliquot of whole blood was placed in modified Dacies fluid (Blaxhall and Daisley 1973) for erythrocyte counting. Erythrocytes were counted by eye in an improved Neubauer chamber after an appropriate dilution. Replicate counts of 1 mm^2 were used to compute the erythrocyte number.

Statistical analysis was with the general linear models procedure of the Statistical Analysis System (SAS). Two-way unequal analysis of variance (ANOVA) was used to determine differences among the three lakes or six collection periods. Differences among individual treatments were tested using Tukey's studentized range test. This test determines whether populations or individual collections were different, but in the absence of an interaction term does not distinguish between combinations of lake and date. The measured variables (hemoglobin, hematocrit, erythrocyte number) were normally distributed, but statistical analyses had to be carried out on logarithmic transformations of the two derived variables (erythrocyte volume and hemoglobin per red cell) which were then normally distributed.

Results

Collection Methods

Collection methods can influence hematological measurements, but the expedient approach we took was best for estimating in situ blood oxygen capacity variables in yellow perch. Hematocrit, mean red cell hemoglobin, and erythrocyte volume changes are more likely as time increases after anesthesia (Lowe-Jinde and Niimi 1983). Hemoglobin concentration varies among groups of rainbow trout that are seined, angled, or electroshocked according to Bouck and Ball (1966); however, their angled group is not comparable with the perch in this study because they were played to exhaustion, anesthetized, and bled 15 min after capture. Railo et al. (1985) found significant red cell swelling in rainbow trout sampled by cardiac puncture after a cephalic blow. Interestingly, the swelling was minimal in whole blood samples that were stored in air for 2 h or more as in the present study. Conflicting results were obtained by Milligan and Wood (1982) who found no difference in hemoglobin or hematocrit between fish sampled from the hemal arch after a cephalic blow and fish cannulated in the dorsal aorta. Casillas and Smith (1977) found that hematocrits increased 14% without a concomitant increase in erythrocyte number after 2 min of angling stress and an additional 1 min prior to sampling. In our study, fish were "in hand" within 20 s and blood collection complete within 1 min, yet the high hematocrits attest to some swelling during capture and sampling.

Intrapopulation, intrasample variability of the measurements was generally large. This appears to be true of fishes in general regardless of sampling technique (Grigg 1974). Perch had to be at least 35 g to obtain sufficient blood for all measurements. This necessarily restricted the size range (12–24.5 cm). Within this range, size did not significantly influence the measured variables, accounting for less than 1% of the variance. Ages and age heterogeneity of the populations differed, however, with Allequash Lake perch in the range sampled averaging 3.5

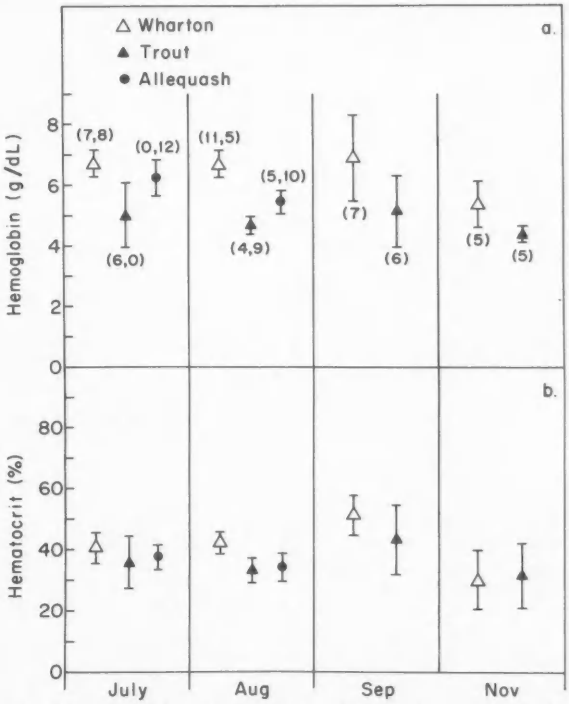

FIG. 1. Hemoglobin and hematocrit levels in the three perch populations during summer and fall of 1983. Means and 95% confidence limits are plotted with the sample sizes in parentheses. There were two collections for both July and August and a single collection in September and November.

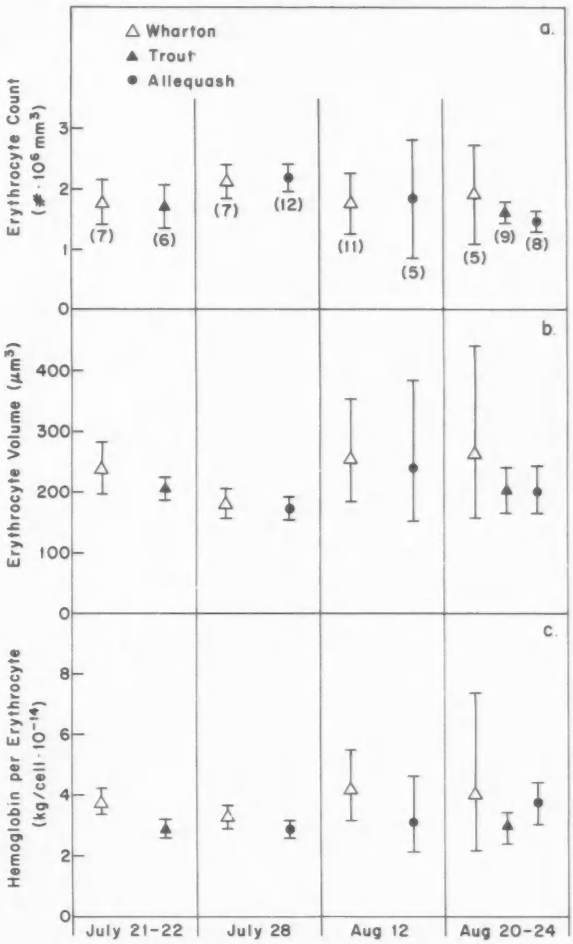

FIG. 2. Erythrocyte numbers and derived variables in the three perch populations during the summer of 1983. Means and 95% confidence limits are plotted with the sample sizes in parentheses. Confidence intervals for the derived measurements are antilogarithms of the corresponding logarithmic limits. Sample sizes for red cell volume and MCHC were identical to the corresponding red cell count.

(±0.69 SD) yr, Trout Lake fish 4.8 (±1.7) yr, and Wharton Lake perch 5.0 (±0.93) yr, possibly accounting for some of the observed differences and variability. Differences in storage time between samples procured at the beginning and end of a sampling day could also have contributed to the variability of the measurements.

Blood Measurements

Hemoglobin

The hemoglobin concentration of blood varied significantly among perch populations (ANOVA, $p < 0.001$) (Fig. 1a). For a given collection, acidic Wharton Lake perch always had the highest hemoglobin concentration, followed in order by perch from Allequash Lake and then Trout Lake. Multiple range testing of the entire data set indicated that perch from each lake differed significantly in hemoglobin concentration from perch in the other two lakes.

Collection date significantly affected hemoglobin concentration (ANOVA, $p < 0.01$), even after removal of two autumn collections from the analysis (ANOVA, $p < 0.05$). The decline in hemoglobin concentration in November produced the large collection effect (Fig. 1). A smaller collection effect came from reduced hemoglobin concentrations in the August 20–24 samples.

Hematocrit

Perch hematocrits varied significantly among lakes from which perch were collected (ANOVA, $p < 0.05$) (Fig. 1). Perch

TABLE 2. Expected results on blood oxygen capacity variables by activating several physiological processes, compared with the observed Wharton Lake differences. + = increase in the blood variable; − = decrease in the blood variable; NC = no expected change in the blood variable.

	Activated process			
Measure	Splenic contraction	RBC swelling	ECF fluid loss	Wharton Lake observed
Hemoglobin	+	NC	+	+
Hematocrit	+	+	+	+
RBC no.	+	NC	+	NC
RBC volume	−	+	NC or −	NC
MCHC	−	NC	NC	+

from Wharton Lake generally had the highest hematocrit, followed by Allequash Lake and then Trout Lake. This trend was not as consistent or obvious as it was for hemoglobin. Multiple range testing of the entire data set indicated that Wharton Lake perch had a higher hematocrit than both Allequash Lake and Trout Lake perch, but the two reference lakes did not differ ($p < 0.05$).

The significant effect of collection date on hematocrit (ANOVA, $p < 0.001$) was caused by large changes in hematocrits during September and November 1983 (Fig. 1). The interaction between collection date and lake was not significant.

Erythrocyte count and derived measurements

Red blood cell numbers did not differ among lakes (Fig. 2a), but did differ with collection date (ANOVA, $p < 0.01$). The date effect was attributable to the higher blood cell counts recorded in fish captured July 28 (Fig. 2a). This collection coincided with the annual thermal maxima for these lakes and followed 2 wk of extremely hot weather for this location (mean air temperature = 23.6°C (± 1.5 SD). The interaction between lake and collection date was not significant.

The logarithm of red blood cell volume did not differ among perch from the three lakes. The erythrocytic volume was lower in fish captured July 28, causing a significant collection effect (ANOVA, $p < 0.01$) (Fig. 2b). There was no interaction between collection date and lake.

The logarithm of hemoglobin concentration per red blood cell (MCHC) varied significantly among the three perch populations (ANOVA, $p < 0.01$) (Fig. 2c). Analysis of the entire data set indicated that acidic Wharton Lake perch had significantly higher hemoglobin concentrations in their red blood cells than did perch from the two circumneutral lakes ($p < 0.05$). Collection date had no influence on the average hemoglobin concentration, nor was there an interaction between lake and collection date.

Discussion

Collection Methods

A possible source of the observed differences between perch populations was a differential response to angling between the three populations. Splenic contraction, erythrocyte swelling, and a shift of extracellular fluid into somatic cells are three components of the stress response that, if operating differentially in one of the populations, could change the interpretation of our results. An examination of Table 2 reveals that none of these three processes, activated differentially in one of the populations, could produce the differences we found in Wharton Lake perch. The larger MCHC seems to be particularly difficult to explain this way. A larger fluid compartment shift in perch from Wharton Lake is most consistent with our results, yet the data of Rask and Virtanen (1986) suggest that any sampling bias in intercompartmental fluid shifts would be in the direction of greater somatic cell water uptake in our circumneutral populations. Such a sampling bias would actually tend to minimize our measured differences compared with actual population differences in hemoglobin, hematocrit, and red blood cell numbers.

Blood Measurements

Lake effects

Hemoglobin, hematocrit, and mean corpuscular hemoglobin (MCHC) differed among perch populations sampled directly from chemically dissimilar lakes in the same lake district. The hemoglobin concentration was statistically distinct among all three populations whereas hematocrit and MCHC differed only in the acid lake. These results correlate with acidity and the seasonal appearance of hypoxic waters; therefore, these two environmental factors will be the focus of our discussion. The reader should be cautioned that many environmental factors covary with pH and dissolved oxygen in natural ecosystems and that some of these may be of importance.

pH effects — Branchial mucus clogging is unlikely to have caused the changes in blood parameters found in acidic Wharton Lake fish. Additional mucus secretion at low pH increases the water–blood diffusive distance, hypothetically limiting the rate at which oxygen can be loaded in the secondary lamellea. Reduced vascular oxygen content or oxygen uptake in fish has been reported under extreme low pH conditions (<4.0) that foster branchial mucus secretion (Packer and Dunson 1972; Ultsch et al. 1980, 1981; Vaala and Mitchell 1970). Our samples were collected at a time when the Wharton Lake pH fluctuates between 4.5 and 5.0, above the range where mucus secretion is commonly observed. The pH in Wharton Lake goes as low as 3.5 in spring, but microscopic examination of gills from Wharton Lake perch captured at the spring pH minimum revealed no unusual mucus secretion (J. A. Nelson, unpubl. obs.). We cannot rule out the possibility that excessive mucus secretion at some early stage of development (Daye and Garside, 1980) selected for fish with greater hemoglobin concentrations and hematocrits.

Depression of blood pH in fish and inhibition of oxygen loading via the Bohr and Root effects may explain the observed changes in blood variables. Investigators have measured acidoses in a variety of fishes exposed to low pH, even at moderate exposure levels and chronic time courses (Lievestad et al. 1976; Neville 1979a, 1979b; Dively et al. 1977; Janssen and Randall 1975; Ultsch et al. 1981). However, measurements of oxygen consumption and vascular oxygen content at these moderate pH doses (4.0–6.0) and measurements of factors that influence blood oxygen capacity during acid exposure have been inconsistent (Lievestad et al. 1976; Neville 1979a; Wood and McDonald 1982). When changes in blood parameters have been reported, it was usually unclear if it was an adaptive response with functional significance or a passive consequence of ion and acid–base imbalances. That administration of adrenaline to acid-exposed rainbow trout has little effect (Milligan and Wood 1982) suggests that there is a large stress component to the hematological responses reported from laboratory studies of acid exposure.

Comparing Milligan and Wood (1982) with our study clearly shows that hematological responses of acutely acid-exposed rainbow trout in the laboratory differ from the interpopulation differences reported here. In trout, hematocrit and red cell number increased concurrently with a reduction in spleen weight and hemoglobin concentration; MCHC was lower in acid-exposed trout. Millgan and Wood (1982) attributed this to a combination of splenic contraction releasing immature erythrocytes (thrombocytes) and red cell swelling. In contrast, perch from acidic Wharton Lake had a higher MCHC accompanying the increased hemoglobin concentration. The Wharton Lake perch response is more like an acclimation to hypoxia (Johansen and Weber 1976) or long-term laboratory acclimation to acidity (C. M. Wood, Department of Biology, McMaster University, Hamilton, Ont., pers. comm.). McWilliams (1982) found no

increase in hemoglobin concentration and slightly larger mean red cell hemoglobin concentrations in an "acid-adapted" population of brown trout (*Salmo trutta*). McWilliams' (1982) conflicting data may result from species differences, the hatchery origin of McWilliams' (1982) fish, different periods of acclimation, and/or the mildness of the acid conditions that they were "adapted" to (pH 5.4–6.6).

We consider the increased hematocrits in Wharton Lake perch to be also part of an adaptive response. Although hematocrits are probably inflated from the collection procedure, the uniformity of our methods among lakes should ensure that swelling was constant across treatments. Most investigators who have measured hematocrits in fish after exposure to low pH have found the increase attributable to the osmotic swelling of erythrocytes and an adrenergic response releasing red cells into the circulation (Milligan and Wood 1982). Although red cell swelling is generally considered a passive response to a concomitant osmotic disequilibrium, it can also be considered part of an adrenergic response to increase blood oxygen affinity (Nikinmaa 1982, 1983). The significantly greater hematocrits in Wharton Lake perch resulted from having slightly more and larger erythrocytes. The similar plasma sodium levels in Wharton Lake and Trout Lake perch (Lyons 1982) suggest that red cells in Wharton Lake perch were not osmotically swollen. In contrast, McWilliams (1982) found increased hematocrits in brown trout adapted to pH 6.0 along with lower plasma ion levels. Rask and Virtanen (1986) produced convincing evidence that the increase in hematocrit from acid lake perch is adaptive. They acclimated European perch (*Perca fluviatilis*) from a naturally acidic lake and a neutral lake to tap water for 3 wk before exposing them to different pH regimes. Significantly greater hematocrits in the acid lake perch at pH levels close to each population's native pH without differences in plasma osmolarity, sodium, or chloride were found. As Rask and Virtanen (1986) lowered the pH to 4.1 and below, further increases in hematocrit were noted for both populations, coincident with plasma ion losses. To explain these and our results, we suggest a two-component process to describe hematocrits in perch from acid environments: (1) an adaptive increase in hematocrit at lake pH levels (~4.5) and (2) red cell swelling resulting from osmotic imbalances, an adrenergic response, or some combination of these at even lower pH values. Further increases could result from a stress response to sampling.

It is likely that perch from naturally acidic lakes exhibit further adaptations in hemoglobin function involving Bohr shifts, intraerythrocytic nucleotide concentrations, pH-insensitive hemoglobin variants, and hemoglobin–oxygen affinity. Willmer (1934) first demonstrated that interspecific differences in Bohr shifts in some tropical fishes were well correlated with the ambient pCO_2. Greater attention needs to be focused on blood chemistry of fish from acid environments.

Oxygen effects — Hemoglobin concentration differences between Allequash Lake and Trout Lake perch could reflect differences in lake oxygenation. While Allequash and Trout lakes have similar water chemistries (Table 1), late summer and winter hypoxic strata occur at depths used by perch only in Allequash Lake. Despite gene flow between these two populations, perch from Allequash Lake had consistently higher hemoglobin concentrations. Again the higher hemoglobin concentration stemmed from more hemoglobin per red cell and not more or larger red cells. Higher hemoglobin levels in Wharton Lake perch suggest that chronic low pH effects are additive with the oxygen effect.

Several studies support our contention that different hemoglobin levels between Trout Lake and Allequash Lake perch resulted from poorly oxygenated habitat present in Allequash Lake only. Krogh and Leitch (1919) observed interspecific differences in hemoglobin function related to the oxygen tension in a fish's environment. European eels (*Anguilla anguilla*), after 2 wk of exposure to hypoxia, increase their blood oxygen capacity 48% (Wood and Johansen 1972). In rainbow trout exposed 3 wk to variations of oxygen, temperature, and photoperiod, low oxygen was the most robust factor stimulating increases in hemoglobin and hematocrit (Tun and Houston 1986).

Seasonal factors

Effects of collection date on blood oxygen capacity variables probably resulted from water temperature changes. There is a tendency for most fishes to have increased blood oxygen capacity at higher temperatures (Chudzik and Houston 1983; Grigg 1974). Yellow perch in northern Wisconsin seem to follow the same pattern, since both hemoglobin and hematocrit were lower in the only collection substantially different in water temperature (November 1983). Water temperature was relatively constant over the previous five sampling periods (Trout Lake 1-m depth mean temperature = 23.4°C (±1.4 SD)). The significantly higher number of red cells of smaller volume for fish captured July 28, 1983, probably resulted from the release of new erythrocytes between then and the previous sampling date (July 21–22, 1983) because the unusually high temperatures during the previous week. In goldfish (*Carassius auratus*), temperature increases stimulate erythropoiesis with a lag time of about 1 wk (Chudzik and Houston 1983).

Conclusions

Naturally acidic Wharton lake (pH range 3.5–5.0) has a perch population with a significantly higher hemoglobin concentration, hematocrit, and mean erythrocytic hemoglobin concentration than fish from two circumneutral reference lakes. The influence of low pH on the blood oxygen capacity variables was in addition to an effect that was attributed to the presence of poorly oxygenated strata used by perch in two of the lakes. Seasonal effects were consistent with previous studies, suggesting higher blood oxygen capacity at warmer temperatures.

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Multivariate Analysis of Correlations Between Environmental Parameters and Cadmium Concentrations in *Hyalella azteca* (Crustacea: Amphipoda) from Central Ontario Lakes

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Stephenson, M., and G. L. Mackie. 1988. Multivariate analysis of correlations between environmental parameters and cadmium concentrations in *Hyalella azteca* (Crustacea: Amphipoda) from central Ontario lakes. Can. J. Fish. Aquat. Sci. 45: 1705–1710.

Cadmium concentrations in *Hyalella azteca* collected from 69 central Ontario lakes ranged from 0.13 to 56.6 μg/g dry mass. Principal components analysis followed by multiple linear regression found three principal components, interpreted as water hardness, total cadmium, and dissolved organic carbon concentrations, to be significantly ($p \leq 0.002$) correlated with cadmium concentrations in *H. azteca*. Cadmium concentrations in *H. azteca* were independent of cadmium concentrations in littoral sediments. It is suggested that cadmium ions compete with calcium ions for uptake sites on the gill surfaces of *H. azteca*. High concentrations of dissolved organic carbon may complex free cadmium ions and reduce their concentration in solution, leading to lower cadmium concentrations in *H. azteca*.

Les teneurs en cadmium chez des spécimens d'*Hyalella azteca* prélevés dans 69 lacs du centre de l'Ontario étaient comprises entre 0,13 et 56,6 μg/g de masse sèche. L'analyse des composantes principales suivie d'une régression linéaire multiple a permis de déceler une corrélation significative ($p \leq 0{,}002$) entre trois grandes composantes (dureté de l'eau, cadmium total et concentration en carbone organique dissous) et les teneurs en cadmium relevées chez *H. azteca*. Les teneurs en cadmium chez *H. azteca* étaient indépendantes de la teneur en cadmium des sédiments littoraux. Ces données semblent indiquer que les ions cadmium rivalisent avec les ions calcium pour les sites de fixation à la surface des branchies chez *H. azteca*. Des teneurs élevées en carbone organique dissous peuvent former des complexes avec des ions cadmium libres et réduire leur concentration dans la solution, ce qui entraîne des teneurs en cadmium plus faibles chez *H. azteca*.

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Except for a local area of high Cd deposition near Sudbury, the central Ontario region has a generally low and uniform Cd deposition rate (Chan et al. 1986). However, low pH has been shown to elevate Cd concentrations in Scandinavian (Henriksen and Wright 1978; Borg 1983) and Ontario (Stephenson and Mackie 1988) lakes. Consequently, Cd concentrations in central Ontario surface waters range from undetectable (<5 ng/L) to concentrations in excess of 500 ng/L (Stephenson and Mackie 1988).

While high environmental Cd concentrations, chiefly in the context of direct industrial contamination, have been related to high concentrations of Cd in biota (Anderson et al. 1978; Kneip and Hazen 1979; Zauke 1981, 1982a, 1982b; Jop and Wojtan 1982), few studies have examined factors modifying the availability of Cd to biota in ecosystems remote from point sources of contamination.

This study examines the effects of the chemical and morphometric characteristics of 69 central Ontario Precambrian Shield lakes on Cd concentrations in the benthic amphipod *Hyalella azteca*. Correlations between Cd concentrations in *H. azteca* and environmental parameters were evaluated by multiple linear regression after the environmental data were reduced to orthogonal variables by principal components analysis (PCA).

Methods

Seventy-five central Ontario lakes (Fig. 1) were sampled between July 17, 1984, and August 15, 1984, by scraping surface sediments with a stainless-steel sieve (0.32 mm) and examining the sediments retrieved for *H. azteca*. *Hyalella azteca* was found in 69 lakes. Animals were sorted with stainless-steel forceps into acid-cleaned polypropylene cups filled with clean lake water. They were kept cool for 24 h to allow gut clearance and then frozen in distilled–deionized water in acid-cleaned polypropylene vials. The animals were subsequently thawed, placed in acid-rinsed polystyrene tissue culture dishes (35 × 10 mm), and examined under a dissecting microscope. Undamaged animals with no observable gut contents (10 per lake when possible) were individually placed in acid-cleaned 1.5-mL polypropylene microcentrifuge tubes and oven dried (55°C)

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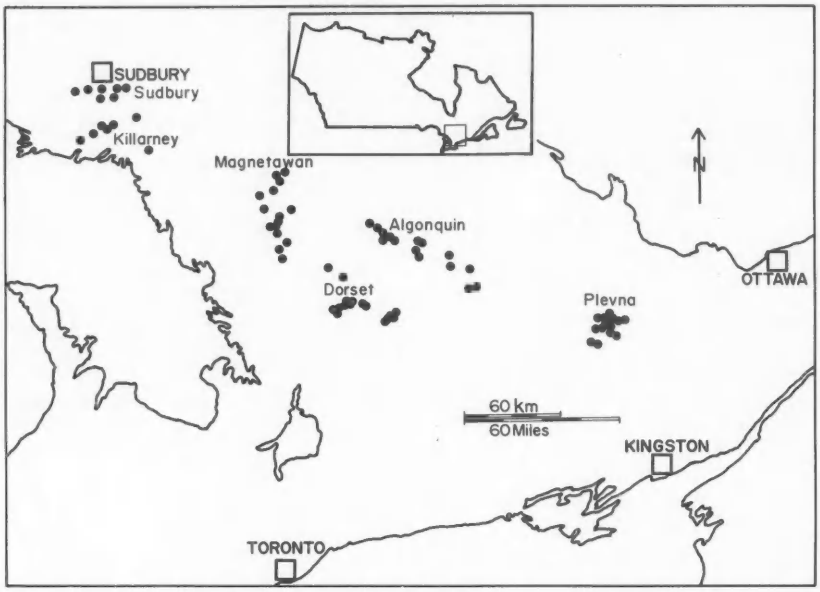

FIG. 1. Central Ontario showing the locations of the study lakes. The square in the inset map of Canada shows the approximate location of the study area.

overnight. Empty vials to be used for analytical reagent blanks were dried simultaneously. After drying, the animals were individually weighed (±5 μg) on a Cahn model G2 electrobalance.

Animals were wet-ashed in microcentrifuge tubes by adding 25 μL of reagent-grade (70%) HNO_3, followed after 1 wk by 10 μL of 50% H_2O_2. The digestate was subsequently diluted with 1.0 mL of distilled–deionized water, giving a sample matrix of 1.7% HNO_3. Reagent blanks and reference materials were digested simultaneously. Digestate solutions were analysed by tungsten furnace atomic absorption spectrophotometry (Scintrex AAZ-2 with Zeeman background correction). The technique was tested by digesting and analyzing Cd concentrations in an NBS standard reference material (1566 oyster tissue). Measured Cd concentrations (3.66 ±0.42 (SD) μg/g dry mass) agreed with the certified value (3.5 μg/g dry mass.

Water samples were collected for routine chemical analysis (Ca^{2+}, Mg^{2+}, Na^+, K^+, Cl^-, SO_4^{2-}, total Fe, total Mn, total P, dissolved organic carbon (DOC)) by the Ontario Ministry of the Environment, using techniques described in Ontario Ministry of the Environment (1981). Lake area, perimeter, and mean and maximum depth were obtained (where possible) from the Ontario Ministry of Natural Resources (Fisheries Branch, Environmental Dynamics Section).

The data were reduced by PCA. The raw data (with the exception of pH) were non-normal, so logarithmic transformations were applied. Box plots (Tukey 1977) indicated that the transformed data were approximately normally distributed. PCA's based upon the correlation matrices, and using varimax rotations, were performed on the normalized data. Stepwise ($p < 0.05$) multiple linear regression was used with mean Cd concentrations in *H. azteca* for each lake as the dependent variable, and PCA scores for each lake on each principal component as independent variables, to identify environmental variables correlated with Cd concentrations in *H. azteca*.

Variables were removed from the data matrix if (1) they loaded most strongly onto a rotated principal component which was subsequently shown by linear regression to be uncorrelated ($p > 0.05$) with cadmium concentrations in *H. azteca* and (2) the mean-square error of the multiple regression run with principal components derived from the reduced data matrix was not significantly different from the mean-square error derived from the original data matrix. The latter was tested using the F-max statistic (David 1952). In this way the original data matrix of 20 variables was reduced to 6 variables loading on three orthogonal principal components, each of which was significantly ($p \leq 0.002$) correlated with Cd concentrations in *H. azteca*.

Results

Cadmium concentrations in *H. azteca* from central Ontario lakes ranged from 0.13 to 56.6 μg/g (Table 1). Water and sediment chemistry and lake morphometric data were available for 51 lakes in which *H. azteca* was found. The 20 variables originally included in the PCA matrix and their means and ranges are given in Table 2. These variables were reduced to six (Ca^{2+}, acid-neutralizing capacity (ANC), pH, Mg^{2+}, DOC, total Cd), loading on three principal components, without any significant ($p < 0.05$) increase in the mean-square error of the regression analysis of variance. The loadings of variables on the three principal components are given in Table 3. These three principal components account for 94% of the overall variance of the six-variable data set and are interpreted as follows: PC1 = Water hardness (Ca^{2+}, Mg^{2+}, ANC, pH); PC2 = DOC; PC3 = total Cd in water. The regression of Cd in *H. azteca* versus the PCA scores for each lake on each principal component is summarized in Table 4. Each principal component is significantly correlated with Cd concentrations in *H. azteca*, and none of the retained variables can be rejected.

TABLE 1. Cd concentrations in *H. azteca* collected from lakes in central Ontario. Unless otherwise noted in parentheses, the number given is the mean of 10 determinations. NP indicates that *H. azteca* was not found at the time of sampling.

Lake	Township	Cd in *H. azteca* (μg Cd/g dry mass)
Richard	Dill	17.8
McFarlane	Broder/Dill	12.3
Raft	Dill/Broder	NP
Lohi	Broder	NP
Clearwater	Broder	NP
Simon	Graham	3.0
McCharles	Graham	4.0
Attlee	Attlee	36.0
Gainey	Attlee	20.7
Broker	Attlee	NP
Tyson	Sale/Attlee	24.0
Mahzenazing	Humboldt	21.7
Kakakiwaganda	Servos	5.12
Ham	Bigwood	1.18
Sollman	Chapman	NP
Cecebe	Chapman	2.2
Ahmic	Chapman/Croft	4.65
Old Man's	Spence	1.36
Bell's (Silver)	Spence	15.6
Spence	Spence	11.0
Horn	Monteith	NP
Bear	Montieth	23.75
Rainey	Ryerson	4.77
Bray	Machar	3.16
King	Machar	18.1
Eagle	Machar	3.18
Deer	Lount	11.3
Lk. M. Islands	Lount	1.35
Whalley	Chapman/Croft	1.92
Canoe	Peck	9.68
McCoy	Sabine	1.4
Hay	Sabine	2.15
McKenzie	Sabine/Lyell	3.87
Lit. Boulter	McClure	1.82
Lk. St. Peter	McClure	2.06
Whitefish	Sproule	5.91
Rock	Nightingale	3.09
Louisa	Lawrence	20.1
Harry	Lawrence	8.41
Cache	Canisbay	4.84
Source	Peck	8.86
Joe	Peck/Hunter	4.51
Potter	Hunter	21.6
Brule	Hunter	24.6
Camp	Miller	1.15
Lucky	Miller	1.05
Ohlmann	Miller	0.13
Reid	Miller	1.28
Big Ohlmann	Miller	1.32 (9)
Dan's	Miller	0.27
Fortune	Miller	0.46
Long Schooner	Miller	0.56
Kitchen	Miller	0.58
Mackie	Miller	0.57
Shaw	Miller	0.22
Brule	Miller	0.40
Grindstone	Miller	0.47
Hill's	Clarendon	0.20 (8)
Buckshot	Miller	0.37 (7)
Echo	McLean	5.54
Ril	Ridout	2.04
Chub	Ridout	20.0
Little Wren	Sherborne	12.6
Beech	Stanhope	1.04
Maple	Stanhope	2.91 (9)
Green	Guilford	2.48
Pine	Guilford	1.09
Cranberry	Guilford	0.97
Harp	Chaffey	4.38
Lake of Bays	Franklin	2.17
Heeney	McLean	37.3
Dickie	McLean	23.6
Plastic	Sherborne	56.5 (1)
Blue Chalk	Ridout	7.23
Red Chalk	Ridout	6.99

The adequacy of the interpretations of the principal components was tested by multiple linear regression using the variables loading on the principal components as independent variables against Cd concentrations in *H. azteca*. Four sets of independent variables were tested (Ca^{2+}, Cd, DOC; ANC, Cd, DOC; pH, Cd, DOC; Mg^{2+}, Cd, DOC). The model including Ca^{2+}, Cd, and DOC has the best fit as measured by the *r*-square, and the regression is summarized in Table 5.

Discussion

Cadmium concentrations in freshwater crustaceans are typically less than 1.0 μg/g dry mass (Zauke 1982b; Jop and Wojtan 1982; Prosi 1983). Concentrations in excess of 2 μg/g are generally associated with industrial contamination (Anderson et al. 1978; Kneip and Hazen 1979; Zauke 1981; Jop and Wojtan 1982; Dallinger and Kautzky 1985). Excluding the value of 56.5 μg/g dry mass obtained for a single specimen from Plastic Lake, Cd concentrations in *H. azteca* from central Ontario lakes ranged from 0.13 to 37.3 μg/g dry mass. Both the highest (Heeney Lake) and the lowest (Ohlmann Lake) concentrations were recorded in remote lakes without known direct sources of contamination.

Multiple linear regression of Cd concentrations in *H. azteca* with the orthogonal-derived variables (principal components) showed that at least three components account for significant amounts of variation. Two principal components (PC2, PC3) have unambiguous interpretations (DOC and total Cd concentrations, respectively). However, PC1 was strongly correlated with Ca^{2+}, Mg^{2+}, pH, and ANC. Its interpretation is ambiguous and must focus on whether hardness cations or ANC (HCO_3^-, CO_3^{2-}) modify the availability of Cd to *H. azteca*.

Interactions between water hardness and trace metal toxicity are well documented. It is thought that the protection afforded by hardness is due to competition between divalent base (Ca^{2+}, Mg^{2+}) and trace metal cations for binding sites, thereby reducing uptake and toxicity. Cadmium toxicity to *Gammarus pulex* is reduced by high Ca concentrations (Wright and Frain 1981), and the process of Cd accumulation has been linked with Ca metabolism (Wright 1980). At "low" Cd concentrations (56 – 560 μg/L), an equimolar relationship between Ca and Cd uptake was implied by Wright (1980). This conclusion is partly supported by data from the present study. Although Cd concentra-

TABLE 2. Variables included in the full PCA matrix, their geometric means, and ranges.

Variable	Mean	Range
ANC (meq/L)	0.0979	0.0025–1.2246
Total P (μg/L)	7.65	3.70–22.0
Ca (mg/L)	4.40	2.09–20.20
Mg (mg/L)	1.05	0.42–4.58
Na (mg/L)	1.11	0.47–24.3
K (mg/L)	0.53	0.24–1.25
F (μg/L)	48.9	26.9–106.9
Cl (mg/L)	0.72	0.03–45.7
SO_4 (mg/L)	7.83	5.12–21.0
Total Fe (mg/L)	0.099	0.022–0.535
Total Mn (mg/L)	0.022	0.003–0.300
DOC (mg/L)	4.74	2.00–15.3
pH	6.74	5.40–8.38
Total Cd in sediment (mg/kg dry mass)	0.076	0.018–2.51
Sediment loss on ignition (%)	1.45	0.300–70.5
Total Cd in water (ng/L)	11.6	2–120
Maximum depth (m)	17.8	3.0–61.0
Mean depth (m)	6.3	1.30–22.2
Lake area (ha)	134.3	8.3–1566.8
Lake perimeter (km)	9.88	1.30–82.0

TABLE 3. Loadings of environmental variables on principal components, and percentage of the overall variance accounted for by each component. Loadings of absolute value greater than 0.50 are underlined.

Variable	PC1	PC2	PC3
Ca	0.965	0.054	−0.179
pH	0.902	−0.048	−0.352
ANC	0.882	0.220	−0.360
Mg	0.874	0.122	−0.114
DOC	−0.087	−0.994	−0.043
Total Cd	−0.312	0.055	0.948
% of total variance	56.51	17.65	19.98

TABLE 4. Stepwise multiple linear regression of log-transformed Cd concentrations in *H. azteca* versus principal components for 51 lakes in central Ontario.

Variable	Coefficient	SE	*t*	*p*
Intercept	0.580	0.039	14.70	<0.001
PC1	−0.424	0.040	−10.64	<0.001
PC2	0.132	0.040	3.31	0.002
PC3	0.342	0.040	8.60	<0.001

$r = 0.899$
$r^2 = 0.808$

Analysis of variance

Source	df	Sum square	Mean square	*F*	*p*
Regression	3	15.717	5.239	66.04	<0.001
Residual	47	3.728	0.079		

TABLE 5. Stepwise multiple linear regression of log-transformed Cd concentrations in *H. azteca* versus Ca, Cd, and DOC in water for 51 lakes in central Ontario.

Variable	Coefficient	SE	*t*	*p*
Intercept	1.182	0.264	4.47	<0.001
Ca	−1.154	0.148	−7.78	<0.001
Cd	0.643	0.101	6.36	<0.001
DOC	−0.805	0.241	−3.35	−0.002

$r = 0.901$
$r^2 = 0.813$

Analysis of variance

Source	df	Sum square	Mean square	*F*	*p*
Regression	3	15.801	5.267	67.92	<0.001
Residual	47	3.645	0.078		

tions in *H. azteca* from lakes in the Sudbury area are high, reflecting the elevated Cd concentrations in lake water, they are not elevated when expressed as a function of the Cd:Ca molar ratio in lake water. The relationship between Cd concentrations in *H. azteca* and the Cd:Ca molar ratio in lake water (Fig. 2) has a slope of 0.843 (SE = 0.072) which is significantly less ($p < 0.05$) than 1. A slope of 1 would suggest that *H. azteca* cannot discriminate between Cd and Ca cations during uptake and excretion. The lower value indicates that some discrimination, either during uptake (i.e. by the cation pump at the gill surface) or via depuration (selective Cd loss during excretion, ecdysis, or other mechanism), may occur.

The second interpretation of PC1 (a gradient of increasing pH and ANC) is the expectation of an interaction between Cd and bicarbonate/carbonate species which could effectively complex Cd and reduce the available cationic fraction of the total Cd concentration. Gardiner (1974) explored Cd speciation with a variety of inorganic and organic ligands, using a Cd-specific electrode. He concluded that there was strong evidence for a soluble Cd–carbonate complex. However, this complex is weak and only forms at pH > 8.0. Under conditions typical of central Ontario lakes, it is unlikely that Cd–carbonate complex formation could significantly modify the Cd bioavailability.

High concentrations of DOC reduce Cd concentrations in *H. azteca*. The effect of DOC on trace metal bioavailability is due to the chelation or complexation of trace metal ions, largely onto humic and fulvic acids (Neubecker and Allen 1983). Laboratory studies (Poldoski 1979; Geisy et al. 1977; Dressing et al. 1982; Winner 1984; Oakden et al. 1984) show that various size fractions of natural dissolved organic matter, or synthetic

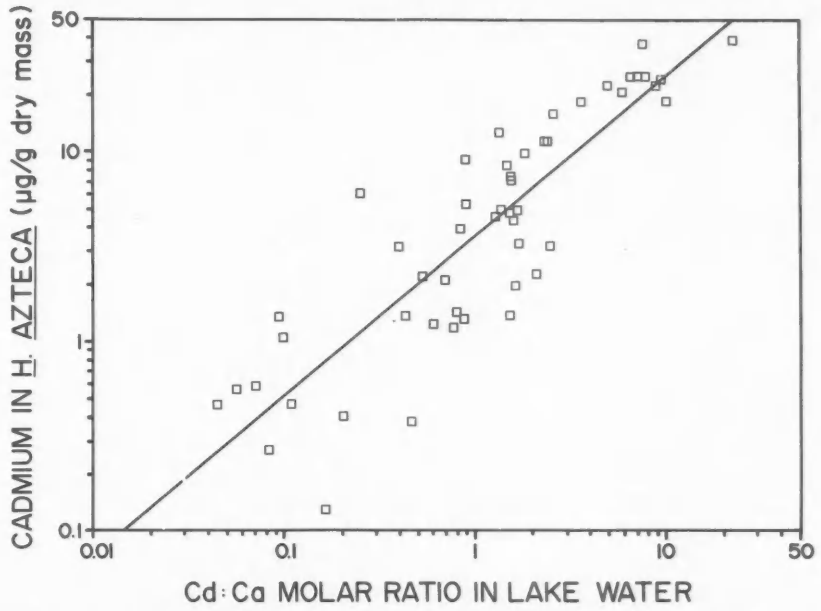

FIG. 2. Cd concentrations in *H. azteca* versus Cd:Ca molar ratios in lake water. The fitted line is described by the equation log (µg Cd/g dry mass) = 0.832 (log Cd:Ca molar ratio) + 0.602 (n = 51, r = 0.86, $p < 0.001$).

chelators, may increase or decrease the bioavailability or toxicity of Cd to invertebrates. The net effect of high DOC concentrations in central Ontario lakes is to decrease the availability of Cd to *H. azteca*, although PC2 (interpreted as DOC) is much less important as a predictor of Cd concentrations in *H. azteca* than PC1 (Ca^{2+}, Mg^{2+}, ANC, pH) and PC3 (total Cd).

Conclusion

Cadmium concentrations in *H. azteca* are correlated with water chemistry and are independent of sediment Cd concentrations and basin morphometry. Three chemical parameters (Ca^{2+}, total Cd, DOC) explain 81.3% of the total variation in Cd concentrations of *H. azteca*. It is likely that Ca^{2+} and Cd compete for uptake, while DOC may complex a portion of the total aqueous Cd, reducing the available ionic Cd concentration.

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Empirical Models Predicting Ingestion Rates of Black Fly Larvae[1]

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Field experiments were performed in a gutter system to examine the effect of body size, water temperature, seston concentration, and particle type on the ingestion rate of *Simulium venustum/verecundum* larvae. Ingestion rates rose exponentially with increasing temperature between 9 and 19°C (Q_{10} = 2.19, 95% CI 2.09–2.29) and rose asymptotically with seston concentration (range 0.7–30 mg·L^{-1}). Small larvae were more sensitive to variations in seston concentration than older instars. The type of particles offered also influenced the ingestion rate of larvae. Once corrected for body size, water temperature, and seston concentration, the data show that larvae ingested more of the natural seston and of a yeast suspension than of suspensions containing kaolinite. Ingestion rates of other simuliid species generally co-occurring at the outflow of lakes in early summer were of the same magnitude as those of *S. venustum/verecundum*, although significant differences were detected among species. Specific ingestion rates of simuliids decline with increasing mass, are similar to those measured for benthic detritivores, and tend to be higher than those of marine and freshwater zooplankton of similar size. The models are discussed with respect to black fly control with particulate larvicides.

Des expériences pratiques ont été effectuées dans des tubes afin d'étudier l'effet de la taille, de la température de l'eau, de la concentration de seston et du type de particules sur le taux d'ingestion des larves de *Simulium venustum/verecundum*. Le taux d'ingestion augmentait de façon exponentielle avec l'augmentation de la température entre 9 et 19°C (Q_{10} = 2,19, IC 95 % = 2,09–2,29) et de façon asymptotique avec la concentration de seston (plage comprise entre 0,7 et 30 mg·L^{-1}). Les petites larves étaient plus sensibles aux variations de la concentration de seston que les stades larvaires plus avancés. Le type de particule influait également sur le taux d'ingestion des larves. Une fois les données ajustées de façon à tenir compte de la taille, de la température de l'eau et de la concentration du seston, les données montrent que les larves ont ingéré une plus grande quantité de seston naturel et de levure en suspension que de suspensions contenant de la kaolinite. Les taux d'ingestion d'autres espèces de simulies qui se trouvaient simultanément à l'exutoire de lacs au début de l'été étaient du même ordre de grandeur que ceux de *S. venustrum/verecundum*, bien que l'on ait relevé des différences importantes entre les espèces. Les taux d'ingestion particuliers des simulies diminuent lorsque la masse augmente, sont semblables à ceux mesurés chez les détritivores benthiques et ont tendance à être plus élevés que ceux d'organismes zooplanctoniques marins et dulçaquicoles de même taille. Les modèles sont analysés en fonction de la lutte contre les mouches noires au moyen de larvicides particulaires.

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Several hundred thousand litres of insecticides are applied each year to control black fly larvae in streams and rivers. Because most of these insecticides are effective only after ingestion by the larvae, the feeding behaviour of larvae is particularly relevant for pest control (Walsh 1985). Studies examining feeding responses of black fly larvae and insecticide efficacy with respect to environmental parameters have indicated the physical properties of insecticide formulations that maximize their efficacy (Kurtak 1978; Guillet et al. 1979; Wenk and Dinkel 1981; Rodrigues et al. 1983). As a result, several highly potent insecticides are available to reduce the nuisance of black flies and to control the populations that carry debilitating human or cattle parasites.

Knowledge of the feeding response of black fly larvae to varying environmental parameters is still fragmentary and no multivariate description exists. Laboratory and field studies have related feeding rates to larval size and physiological state, type and concentration of suspended material, and temperature; these responses can vary among species (Ladle et al. 1972; Elsen and Hébrard 1979; Lacey and Mulla 1979; Schröder

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1980). However, these observations have yet to be synthesized into quantitative descriptions that allow a ranking of the relative importance of each factor in determining feeding rate in natural conditions. Such a synthetic description could then be used to determine more accurately the necessary dosage of insecticides, thus minimizing operational costs and impact on nontarget species; it would also help to quantify more precisely the role that black fly larvae play in the transport and processing of suspended material in running water systems.

The goal of this study was to measure the feeding rate of larvae of *Simulium venustum/verecundum* at various temperatures and seston concentrations and then to synthesize these descriptions in a multiple regression model. We also examined how the type of offered particles influences feeding rate and compared the response of other species of simuliids and invertebrates with the responses of *S. venustum/verecundum*. The implications of the observed relations are then discussed with respect to control of simuliids with particulate larvicides.

Materials and Methods

Experimental Design

The study was performed in a gutter system at the confluence of Ruisseau Boitel, the outlet of Lac Boitel, and the Rivière Mattawin, in the Réserve Saint-Maurice, Quebec (46°57′N, 73°02′W). The gutter system, a multiple version of that described in Morin et al. (1988), consisted of four large plastic sinks filled continuously by gravity with water from Ruisseau Boitel and 12–16 sections (1.5 m long, 10 cm wide) of vinyl gutter fed from short pipes fixed to the drains of the sinks. Discharge in the gutters was controlled so that average current velocity in the gutters was 40–50 $cm \cdot s^{-1}$. Concentration of natural seston in the stream varied from 0.7 mg dry $mass \cdot L^{-1}$ at the lowest discharge of Ruisseau Boitel to 6 $mg \cdot L^{-1}$ during a major storm. To increase the range of seston concentrations, we added suspended material in the gutters for some experiments. Three types of suspensions were utilized: an organic suspension of brewer's yeast (*Saccharomyces cerevisiae*, cell diameter 6–20 μm), an inorganic suspension of kaolinite (particle diameter <2 μm), and a mixture of powdered rabbit feed (particle diameter 10–250 μm) and kaolinite. In experiments where particles were added to the natural seston of Ruisseau Boitel, we filled Mariotte bottles, which empty at a constant rate, with a concentrated suspension of particles and connected these bottles to the pipes draining the sinks with a piece of Tygon tubing.

Experiments were performed during May and June in 1986 and 1987. Before each experiment, simuliid larvae were collected from the outflow of Lac Boitel, from the outflow of neighbouring lakes, or from the Rivière Mattawin and transported live in buckets to the gutter system. Larvae were then transferred to the gutters and left to acclimate for at least 6 h. At the beginning of the experiments, a suspension of Norite (fine-grained charcoal) was added at the gutter inlet for 3 min. This pulse marks the beginning of the experiment as a black band in the gut of the animals. The larvae were then left to feed for 5–10 min. At the end of the feeding period, the gutters received a second 3-min pulse of Norite to mark the end of the feeding period. Larvae were collected 5–10 min after the end of the second application of Norite and preserved in 4% formaldehyde. In experiments with added suspended material, the Mariotte bottle was unplugged at the beginning of the feeding period.

TABLE 1. Results of the experiments on ingestion of *S. venustum/verecundum*. Listed are the water temperature (T, in °C), the seston concentration ([s], in mg dry $mass \cdot L^{-1}$), the intercept (a), the slope (b), and their standard error (SE), the coefficient of determination (r^2), the residual mean square (RMS), and the number of larvae examined (n) to fit the model log (ingestion rate, in $mm^3 \cdot min^{-1}$) = $a + b$ log (body length, in mm).

Date (yr-mo-d)	T	[s]	a	SE	b	SE	r^2	RMS	n
Natural seston only									
860513	14	0.9	−5.52	0.08	3.22	0.22	0.72	0.128	87
860513	16	0.7	−5.48	0.09	3.33	0.16	0.81	0.133	99
860514	18	1.0	−5.27	0.06	3.41	0.11	0.91	0.073	98
860519	12	1.4	−4.78	0.12	2.97	0.20	0.74	0.044	80
860520	12	3.3	−4.65	0.08	2.54	0.13	0.81	0.060	96
860526	18	1.5	−4.07	0.09	2.34	0.14	0.75	0.027	93
860530	18	3.6	−4.22	0.07	2.39	0.11	0.80	0.048	121
870512	10	1.5	−4.71	0.04	2.62	0.06	0.92	0.035	156
870513	8	1.4	−4.76	0.04	2.45	0.07	0.89	0.034	155
870513	13	4.2	−4.60	0.05	2.43	0.08	0.85	0.058	154
870514	13	5.9	−4.36	0.08	2.26	0.12	0.75	0.029	118
870514	13	5.4	−4.25	0.07	2.12	0.10	0.77	0.024	127
870514	13	6.0	−4.31	0.07	2.22	0.10	0.80	0.021	120
Natural seston + kaolinite + rabbit feed									
860519	12	23.1	−4.49	0.08	2.61	0.15	0.76	0.052	102
860519	12	7.3	−4.48	0.09	2.35	0.15	0.72	0.058	100
860520	12	29.6	−4.50	0.05	2.43	0.09	0.87	0.047	101
860526	19	7.7	−4.35	0.09	2.40	0.14	0.73	0.042	108
860530	18	5.9	−4.10	0.17	2.00	0.25	0.42	0.068	91
860530	18	9.4	−3.98	0.19	1.84	0.28	0.28	0.116	113
860602	14	30.7	−4.23	0.07	1.96	0.12	0.70	0.047	123
Natural seston + yeast									
870512	10	4.5	−4.55	0.03	2.49	0.06	0.92	0.029	159
870512	10	6.6	−4.49	0.04	2.35	0.07	0.88	0.035	153
870512	10	7.7	−4.53	0.03	2.45	0.06	0.93	0.019	140
870512	10	9.2	−4.45	0.04	2.36	0.06	0.90	0.028	149
870512	10	11.5	−4.45	0.03	2.40	0.06	0.91	0.029	144
870512	10	14.8	−4.49	0.03	2.50	0.05	0.94	0.020	154
870514	13	7.5	−4.22	0.08	2.25	0.12	0.75	0.030	127
870514	13	9.5	−4.10	0.06	2.16	0.09	0.84	0.015	120
870514	13	11.7	−4.15	0.07	2.21	0.10	0.80	0.021	118
Natural seston + kaolinite									
870513	8	3.0	−4.81	0.04	2.58	0.07	0.90	0.033	148
870513	9	5.4	−4.73	0.04	2.47	0.07	0.90	0.029	164
870513	10	5.9	−4.80	0.05	2.50	0.08	0.87	0.041	149
870513	10	7.8	−4.82	0.05	2.56	0.09	0.87	0.045	130
870513	11	9.9	−4.75	0.03	2.56	0.06	0.93	0.025	144
870513	11	11.7	−4.98	0.05	2.76	0.08	0.88	0.059	149

Measurements

The water in the gutters was sampled at the beginning, middle, and end of each experiment and the concentration of seston measured by filtering 200–250 mL of water on preweighed Nuclepore filters (0.2-μm pore diameter). Filters were kept frozen (−20°C) until return to the laboratory, where they were

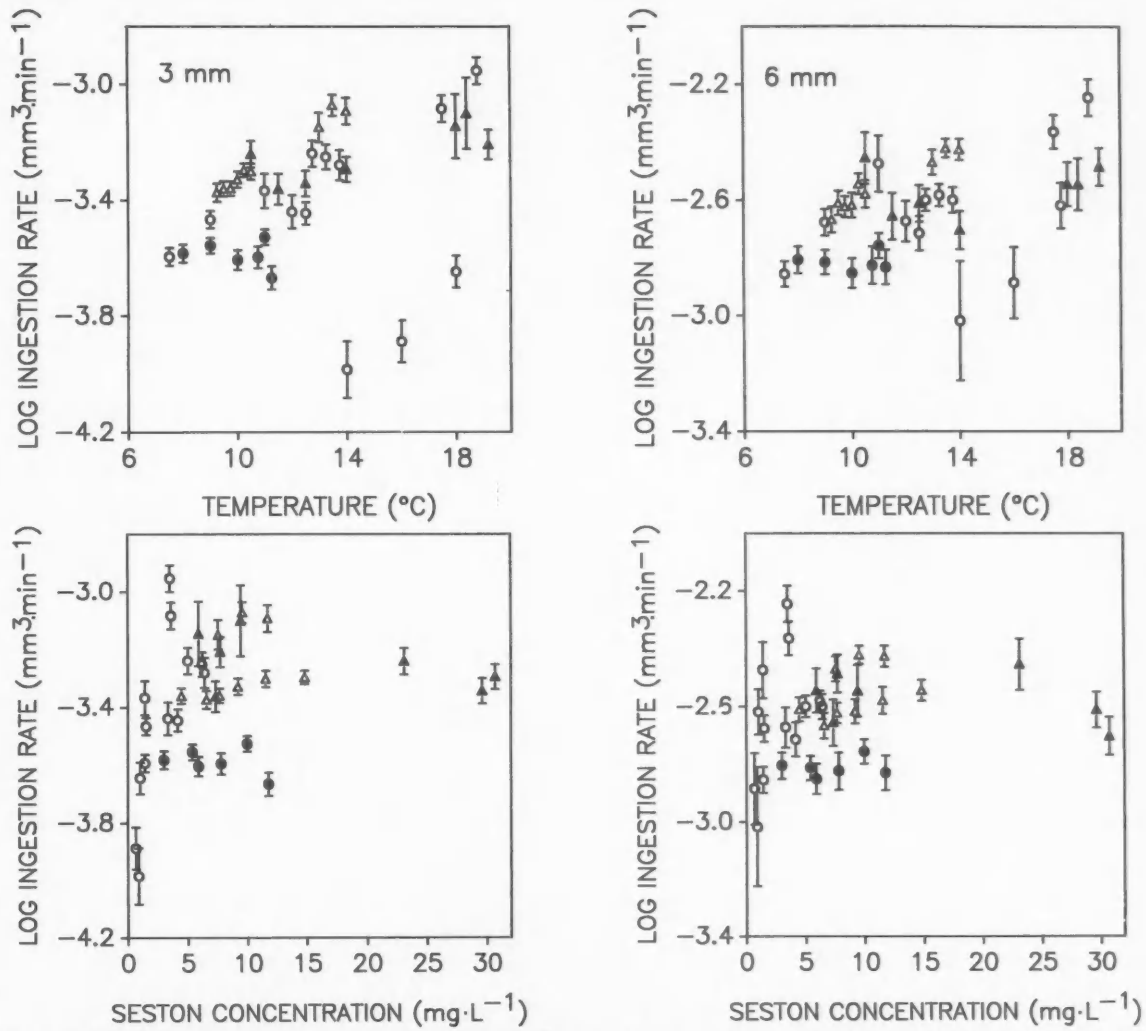

FIG. 1. Effect of temperature and seston concentration on the ingestion rate of *S. venustum/verecundum* larvae. Each data point represent the estimated mean ingestion rate of 3- or 6-mm larvae in each experiment calculated from the regressions presented in Table 1. The vertical bars represent the 95% confidence interval for the mean. The various symbols represent the results with the different types of particles: natural seston only (open circles), natural seston + kaolinite (solid circles), natural seston + yeast (open triangles), and natural seston + kaolinite + rabbit feed (solid triangles).

dried for 24 h at 60°C. After cooling in a desiccator, filters were reweighed to the nearest microgram on a Cahn electrobalance. Seston concentration during experiments did not vary more than by 10%, about the magnitude of measurement error, and mean concentration was used for all calculations.

Feeding rates of larvae were measured as the volume of gut filled per unit time. We measured the body length of each larvae and the length (to the nearest 0.1 mm) and diameter (to the nearest 0.02 mm) of the portion of the gut enclosed between the two Norite bands. Because the gut is cylindrical, this sufficed to estimate the volume ingested. In a few experiments, the first band of Norite had already been egested by the smallest larvae by collection time, and for those experiments, we completely eliminated the data for the smallest size classes. Larvae were identified according to the criteria of Wood et al. (1963), but species that could not be distinguished at all instars were grouped.

Data Analysis

For each experiment, the feeding rates of *S. venustum/verecundum* in each experiment were first fit to the model

$$(1)\quad \log \mathrm{IR} = a + b \log L$$

where IR is the volume of gut filled per unit time (cubic millimetres per minute) and L is the body length (millimetres, range 0.7–6.5 mm). Logarithms are required to stabilize the variance and linearize the regressions. To compare feeding rate among experiments and describe the shape of the relationship between

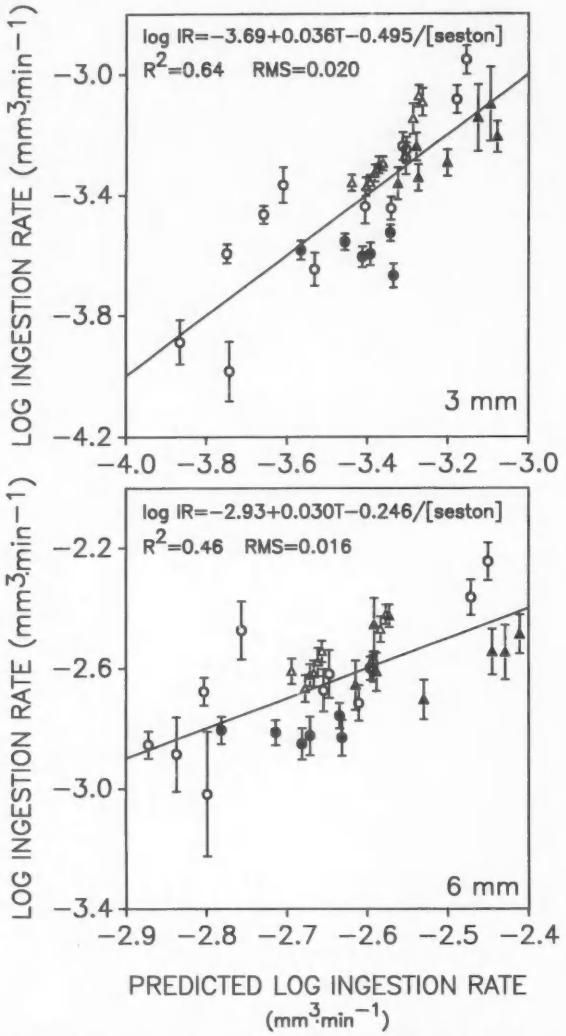

FIG. 2. Estimated mean ingestion rate of 3- and 6-mm larvae of *S. venustum/verecundum* versus the values predicted by the multiple regression model including water temperature and the inverse of seston concentration. Symbols as in Fig. 1.

feeding rate and water temperature and seston concentration, we first calculated the mean feeding rates of small (3 mm) and large (6 mm) larvae using the regression equations (Table 1) calculated for each experiment. These values were used to establish the shape of the relation between feeding rate and temperature and seston concentration. This done, a multiple regression model was estimated from the individual observations for *S. venustum/verecundum*. Residuals of that regression model were then examined to detect whether particle type influenced feeding rate.

Results and Discussion

Simple Regression Models

Regressions describing feeding rate in the 35 experiments are presented in Table 1. In all experiments, feeding rate was positively correlated with body length ($P < 0.0001$ for all regressions). The residual variance of these experiment-specific regressions (RMS in Table 1) varied from 0.02 to 0.13. Feeding rates for individual larvae varied from half to twice the mean response (corrected for body length), in the best case where the fit to the regression was the tightest, up to one fifth to five times the mean in experiments where the residual variability was the highest (mean 35–270%). Intercept, slopes, and predicted mean feeding rates differed significantly among experiments (Fig. 1).

TABLE 2. Multiple regression models predicting ingestion rates of *S. venustum/verecundum*. Listed are the coefficients, their standard error (SE), the standard partial regression coefficient (Std β), the number of data points (n), the coefficient of determination (R^2), and the residual mean square (RMS). Both models include log body length (LL, in mm), water temperature (T, in °C), the inverse of seston concentration (1/[s], in L·mg⁻¹), and the interaction between LL and 1/[s]). In addition, Model 2 includes dummy variables for seston type (KR = kaolinite + rabbit feed, Y = yeast, K = kaolinite). All coefficients are highly significant ($P < 0.001$)

	Model 1			Model 2		
	Coefficient	SE	Std β	Coefficient	SE	Std β
Constant	−4.887	0.019	0.000	−4.770	0.023	0.000
LL	2.399	0.023	0.771	2.364	0.022	0.759
T	0.037	0.001	0.172	0.034	0.002	0.159
1/[s]	−0.583	0.020	−0.413	−0.628	0.019	−0.444
LL/[s]	0.601	0.038	0.229	0.611	0.035	0.233
KR				−0.108	0.012	−0.063
Y				0.036	0.011	0.026
K				−0.217	0.012	−0.137
n	4498			4498		
R^2	0.84			0.86		
RMS	0.064			0.055		

Multiple Regression Models

Scatter diagrams suggested that water temperature and seston concentration positively affected feeding rate (Fig. 1), and this was confirmed by multiple regression analysis of feeding rate with water temperature and the inverse of seston concentration as independent variables (Fig. 2). Water temperature had approximately the same influence on feeding rate of small and large larvae (95% CI of Q_{10} = 1.9–2.8 and 1.7–2.3, respectively). However, the coefficient for the inverse of seston concentration differed significantly between the two sizes (95% CI for coefficient = 0.375–0.615 for 3-mm larvae, 0.118–0.374 for 6-mm larvae). Thus, the response to variations of seston concentration apparently varied with size.

To integrate these observations, a multiple regression model including body length, temperature, seston concentration, and an interaction term for the joint effects of body length and seston was fitted to the individual observations (Table 2). This model explained 84% of the variance among individual measurements of feeding rates, and 95% of the observations lie within approximately 30–320% of the predicted value (Fig. 3). The interaction between body length and seston concentration was highly significant, confirming the trend observed with estimates of mean feeding rate. Other interaction terms (length–temperature, temperature–concentration, temperature–concentration–length) were not significant (sequential F-test, $P > 0.05$).

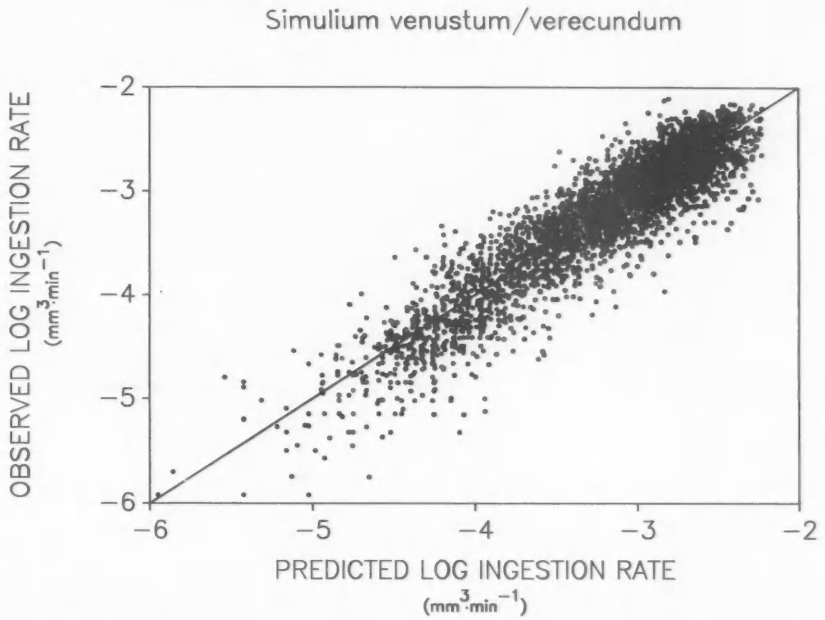

FIG. 3. Observed individual ingestion rate of *S. venustum/verecundum* versus the values predicted from Model 1 in Table 2 (n = 4498).

Effect of Water Temperature

Feeding rate of *S. venustum/verecundum* rises with increasing temperature and approximately doubles between 10 and 20°C. This is similar to the feeding response of *Simulium vittatum* on natural seston between 10 and 19°C (Lacey and Mulla 1979). Schröder (1981) observed that *Simulium ornatum* (cited as *Odagmia ornata*) feeding on *Nitzschia* labelled with ^{14}C increased approximately sevenfold from 5 to 15°C. However, Ladle et al. (1972) found no increase in feeding rate between 8 and 21°C for *S. ornatum* whereas Elsen and Hébrard (1979) found that feeding rate of *Simulium damnosum* s.l. peaked at 25°C.

Direct comparison of these results is difficult. Since feeding rates of individual larvae have a lognormal distribution (Fig. 4, where the abscissa is logarithmic) and can vary from 50 to 200% of the mean feeding for similar larvae, one needs a relatively large number of values to obtain a precise estimate of mean feeding rate. Schröder's (1981) results are suspicious, since he excluded data points that appeared to be outliers on an arithmetic scale from his calculations. Ladle et al. (1972) reported neither the number of larvae examined nor the variability among larvae; therefore the absence of a temperature response may be real or reflect high variability and small sample size. Elsen and Hébrard (1979) sampled at a range of warm temperatures that does not overlap with ours, and therefore, we do not have the data to determine if *S. venustum/verecundum* ingestion also peaks above 20°C. Lacey and Mulla (1979) reported statistics necessary for comparison and their results are consistent with ours. Thus the most completely described results suggest that the ingestion rate of simuliids doubles from 10 to 20°C.

Effect of Seston Concentration

The ingestion rate of *S. venustum/verecundum* rises asymptotically with increasing concentrations of seston, and small larvae respond more than large ones to differences in seston concentration (Fig. 5). In most cases, larvae feed at a rate close to the maximum. However, ingestion rates could be limited by seston concentration but only when seston concentration in the natural habitat of *S. venustum/verecundum* drops below 1–2 mg·L^{-1}. Since these are extreme values for lake outlets (A. Morin, pers. obs.), it appears that only the feeding of the smallest larvae is likely to be affected by seston concentration in natural conditions.

Effect of Particle Type

Particle type also influenced feeding rate (Fig. 4). After correction for the effect of body length, water temperature, seston concentration, and the interaction of body length and seston concentration, it appeared that larvae ingested a significantly smaller volume of kaolinite and of kaolinite plus rabbit feed than of the yeast suspension. The feeding rate of larvae on natural seston was intermediate. Of the three artificial diets tried in this experiment, the yeast suspension yielded estimates that were the closest to those measured with natural seston. This trend was confirmed by analysis of covariance with dummy variables (Draper and Smith 1981; Table 2). Thus, the best model included all parameters. The Q_{10} estimated from this model was 2.19 (95% CI = 2.09–2.29).

Simulium venustum/verecundum ingested larger volumes of organic particles (yeast) than of inorganic particles (kaolinite). This may either reflect a response to digestibility of material or, more simply, differences in the catchability of particles. Schröder (1981) showed that feeding rate of larvae depends on the type of particles and interpreted the differences as reflecting differential capture efficiency for particles of different size. Because the type of offered particles influences feeding rate, estimates of feeding obtained with synthetic diets may not reflect responses in natural situations.

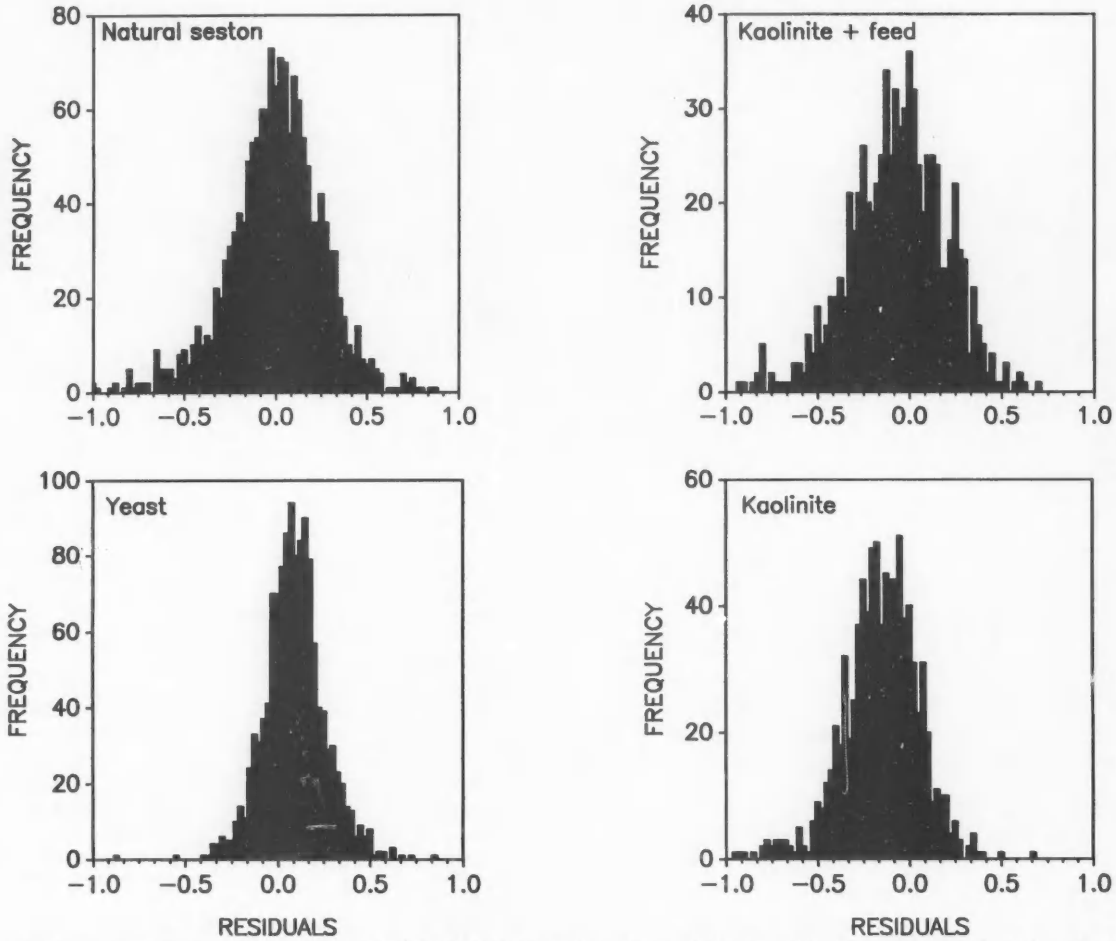

FIG. 4. Frequency distributions of the residuals to Model 1 (Table 2; Fig. 3) for each type of offered particles. Note that the abcsissa is logarithmic, so that the apparently normal distributions are in fact lognormal.

Other Species

Feeding rates of other species of simuliids were of the same magnitude as those of *S. venustum/verecundum* (Fig. 6). However, because the study permitted a large number of individual estimates, even small differences between the observed feeding rate for these other species and the predictions from Model 2 for *S. venustum* usually proved significant (Table 3). On average, *Cnephia dacotensis* ingested only 80%, *Stegopterna mutata* 95%, *Simulium decorum* 102%, *S. croxtoni/aureum* 120%, *S. tuberosum* 150%, and *S. corbis* 170% of the volume ingested per unit time by *S. venustum/verecundum*.

Although the model seemed to consistently under- or overestimate depending on the species, observations were linearly related to predictions, and the error around this linear relationship was similar to the measurement error. Other species of simuliids therefore appear to respond to temperature and seston concentration as does *S. venustum/verecundum.*, although on average they ingest somewhat more or less volume per unit time. These differences may reflect differences in the ultrastructure of the cephalic fans (Ross and Craig 1980) or preferences for different microcurrent velocities (Morin et al. 1986).

The application of *S. venustum/verecundum* model to other species of simuliids requires caution. Apparently, the shape of the response curves of feeding to temperature and seston concentration do not differ greatly among species. Thus, the model adequately predicts the relative change of feeding rate with changes of temperature or seston concentration. However, the predicted values are biased, and regression models would have to be estimated for each species separately to obtain more accurate estimates.

The generality of the feeding rate model can be more critically assessed by comparing its predictions with values obtained by other researchers (Fig. 7). The scatter around the 1:1 line in Fig. 7 is large, reflecting the effect of other factors. Observations from Schröder (1981) with *S. ornatum* and Hart and Latta (1986) with *Prosimulium mixtum/fuscum* are not even correlated with predictions. In both studies, larvae were fed artificial diets with uniform-sized particles. By contrast, observations from the three other studies of feeding on natural seston are

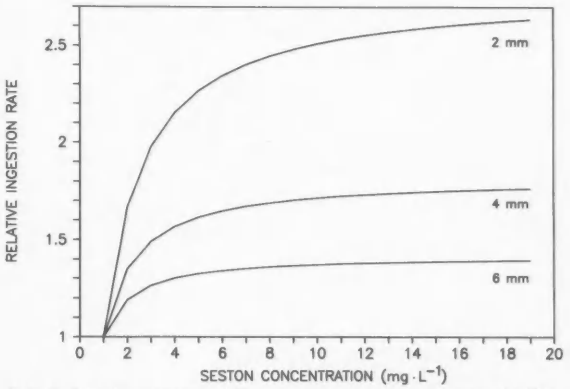

FIG. 5. Feeding response of *S. venustum/verecundum* larvae of different sizes to increase in seston concentration. The ordinate axis is the ratio of feeding rate at a given seston concentration to the feeding rate of larvae of that size at a concentration of 1 mg·L^{-1}. Derived from the regression equation of Model 2 solved for natural seston at 15°C.

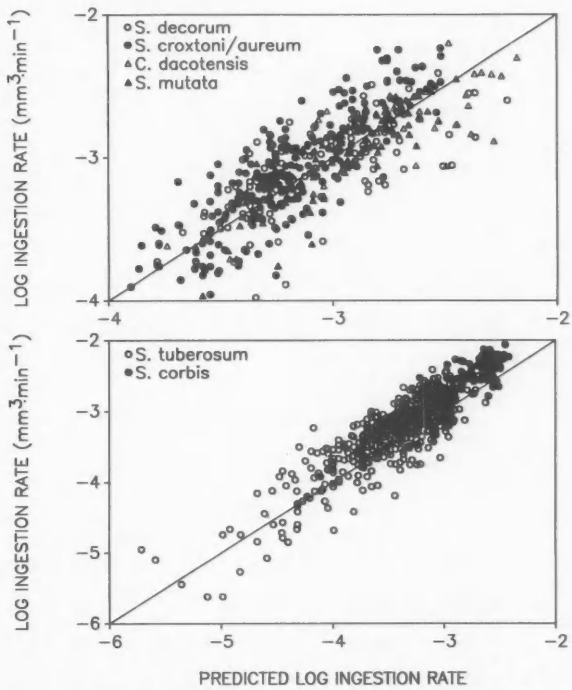

FIG. 6. Observed individual ingestion rate of other species of simuliids versus the values predicted by the best model (Model 2, Table 2) for *S. venustum/verecundum*.

significantly correlated with predictions. More data are required to distinguish between the hypotheses that the model does not fit the response of *S. ornatum* and *P. mixtum/fuscum* or that ingestion estimates obtained in the laboratory on artificial diets are unconnected to ingestion in the natural habitat. The estimates of Elsen (1980) for *S. damnosum* are particularly well correlated with predictions of the model, but are 10 times higher. *Simulium damnosum* is a large river species that lives in watercourses where seston concentration and water temperature are noticeably higher than the range of conditions sampled in this study.

Compared with other invertebrates of similar size, *S. venustum/verecundum* eat approximately 10 times more material per unit time than zooplankton and roughly the same amount as detritivores and a shredder (*P. proteus*; Fig. 8). Lower feeding rates of zooplankton may reflect some selectivity for nutrient-rich particles that can be digested, or simply the more nutritious food available to them (Peters 1984).

The longitudinal distribution of species along the gradient from lake outlets to larger rivers seems to correlate with their feeding rates. Other things being equal, strict lake outlet species (*C. dacotensis*, *S. mutata*, and *S. decorum*) had the lowest feeding rates whereas the only large river species sampled (*S. corbis*) had the highest feeding rate. *Simulium tuberosum* had the second highest feeding rate; this species is found from lake outlets to large rivers where it co-occurs with *S. corbis*. We hypothesize that this gradient in feeding rate reflects seston nutritive quality. The proportion of organic matter in seston decreases with increasing distance from the lake in outlets, as does the "quality" of the seston measured by its protein content (Morin 1987). To obtain a similar amount of energy and nutrients per unit time, species distributed far downstream of lakes or in large rivers therefore have to process a larger amount of material.

Practical Implications for Black Fly Control

The trends observed in this study have several implications for black fly control. It is generally assumed that mortality of larvae is proportional to the amount of larvicide ingested. The increase in feeding rate with increasing temperature implies that for the same amount of insecticide, mortality will be higher at warmer temperatures, even without a change in the specific activity of the insecticide. Knowledge of the feeding response of simuliids to temperature is essential to the study of temperature effects on different formulations independent of feeding rate.

More relevant to operational situations is the effect of natural seston concentration on efficacy of particulate formulations. Because feeding of larvae is not linearly related to seston concentration and reachs its maximum at low concentrations, it is necessary to adjust the amount of insecticide for seston load. Above 4–6 mg·L^{-1}, feeding rate of *S. venustum* is independent of seston concentration, and the quantity of larvicide ingested will be directly related to the proportion of larvicide in the total pool of particulates. Thus, twice the amount of formulation will be required at 20 mg·L^{-1} compared with what is required at 10 mg·L^{-1} to achieve the desired mortality rate. For other target species, which may differ in their response to seston concentration, this simple rule may have to be modified.

The feeding rates of simuliid larvae also have important consequences for the screening and development of new larvicide formulations. Bioassay procedures need to be standardized to obtain meaningful comparisons and results. Feeding rates of larvae on artificial diets may not reflect rates in natural conditions and may therefore select for formulations that are operationally ineffective. Bioassays in the field are also difficult to compare without accounting for the effects of body size, temperature, and seston concentration. Regression models similar to those presented here should be used to standardize results when it is not possible to control for temperature and seston.

TABLE 3. Comparison of observed ingestion rates for the other species of simuliids with the predictions of Model 2 for *S. venustum/verecundum*. Listed are the number of observations (n), the mean residual value (MR, observed minus predicted) and its variance (s^2), the coefficient of determination (r^2) and the residual mean square (RMS) of the regression log (observed) = a + b log (predicted), and the F-value (with 2, $n-2$ df) and associated probability of the hypothesis that $a = 0$ and $b = 1$ (Seber 1977). Predictions of Model 2 are adequate for species other than *S. venustum* when the mean residual value is not significantly different from 0 and when the intercept and slope of the regression of the observations against the predictions are not significantly different from 0 and 1, respectively. This is the case for *S. mutata* only.

Species	n	MR	s^2	r^2	RMS	F	P
C. dacotensis	35	−0.100	0.054	0.61	0.044	8.26	0.001
S. mutata	103	−0.025	0.024	0.82	0.024	1.71	0.186
S. decorum	128	0.008	0.058	0.62	0.052	8.16	<0.001
S. croxtoni/aureum	255	0.081	0.046	0.75	0.046	20.43	<0.001
S. tuberosum	655	0.171	0.060	0.74	0.059	162.7	<0.001
S. corbis	89	0.231	0.035	0.37	0.034	71.62	<0.001

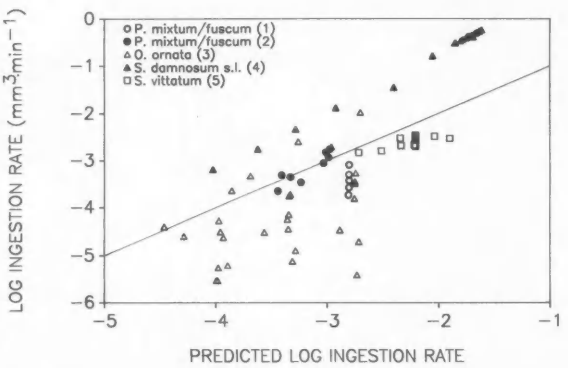

FIG. 7. Comparison of published values of feeding rate of simuliids with the predictions of Model 2 for *S. venustum/verecundum*. Author, type of offered particles, and experimental conditions: (1) Hart and Latta (1986), pollen, 5-mm larvae, 6.5°C, 25–200 mg·L^{-1}, (2) this study, natural seston, 4.5- to 9-mm larvae, 6–18°C, 0.7–14.8 mg·L^{-1}, (3) Schröder (1981), algal cultures labelled with ^{14}C, 1.5- to 4.7-mm larvae, 15°C, 0.8–12 mg·L^{-1}, (4) Elsen (1980), natural seston, 0.9- to 8.6-mm larvae, 28°C, 30 mg·L^{-1}, (5) Lacey and Mulla (1979) fluorescent dye and finely ground laboratory chow, 6.5-mm larvae, 4–28°C, 1–100 mg·L^{-1}.

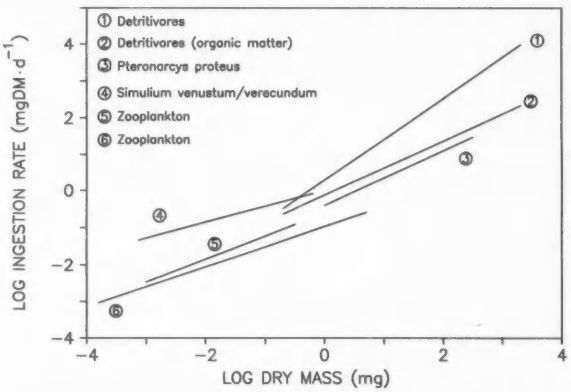

FIG. 8. Relationship between feeding rate and body mass for *S. venustum/verecundum* and for other invertebrates. The lines represent either solutions of multiple regression models at 15°C and 2 mg·L^{-1} or the direct allometric relation described at 15°C. Note that *S. venustum/verecundum* ingest about 10 times more material than zooplankton of similar size and apparently a similar amount as detritivores. Data from sources: (1) Cammen (1980), (2) Cammen (1980), (3) Perry et al. (1987), (4) this study, (5) Ikeda (1977), (6) Peters and Downing (1984).

The use of larvae of the same instar to "standardize" body size may not be efficient, since the individual mass can vary by about threefold (A. Morin, unpubl. data). Moreover, selecting only animals of the same size may constrain the supply of bioassay animals unnecessarily, since the regression approach would allow use of animals of various sizes and control for the size effect.

Acknowledgements

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Biological Bases for Mixed-Species Fisheries: Species Co-distribution in Relation to Environmental and Biotic Variables

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Murawski, S. A., and J. T. Finn. 1988. Biological bases for mixed-species fisheries: species co-distribution in relation to environmental and biotic variables. Can. J. Fish Aquat. Sci. 45: 1720–1735.

Factors influencing the degree of temporal and spatial co-occurrence of seven important demersal fish species on Georges Bank (Northwest Atlantic) were analyzed. Species/age co-occurrence data from a 24-yr time series of research vessel bottom trawl surveys were evaluated in relation to temperature and depth preferences, spatial distribution, and species/age abundance trends. Co-occurrence of various species/age groups varied greatly by season and was significantly correlated with overlap in temperature/depth preference indices and annual species abundance. Although species abundance and proportion of survey tows having particular species varied widely over the time series, trends in spatial dispersion indices of particular species were not generally related to abundance. Multiple regression models incorporating temperature and depth preference overlap and species abundance as independent variables accounted for a high proportion of total variance in the transformed proportion of survey tows containing co-occurring species (mean $R^2 = 0.69$ for age 1+ fishes, mean $R^2 = 0.44$ for age 0). Results indicate that although the frequency of technological (bycatch) interaction among pairs of species may be highly variable depending on season, area, and year, co-occurrence among species is nonetheless relatively predictable. Minimization of the potential adverse impacts of mixed-species harvesting (i.e. failure to achieve management goals for all species simultaneously) may be accomplished by exploiting stocks individually during periods of maximum spatial separation and by using information on the determinants of species co-distribution to more accurately forecast bycatch levels.

Les facteurs influant sur le niveau de présence spatio-temporelle simultanée de sept espèces importantes de poissons démersaux sur le banc Georges (Atlantique nord-ouests) ont été analysés. Les données sur la présence simultanée selon l'espèce et l'âge provenant d'une série chronologique de 24 a obtenue à partir de campagnes de recherche à bord d'un chalutier de fond ont été évaluées en fonction des préférences de température et de profondeur, de la répartition spatiale et de tendances de l'abondance en fonction de l'espèce et de l'âge. La présence simultanée de divers groupes d'espèces et d'âge variait beaucoup d'une saison à l'autre, et elle était fortement corrélée à un chevauchement des indices de préférence de température et de profondeur et de l'abondance annuelle des espèces. Bien que l'abondance de l'espèce et la proportion de traits de chalut contenant une espèce particulière variaient énormément au cours de la série chronologique, les tendances des indices de la répartition spatiale d'une espèce donnée n'étaient pas liées en général à l'abondance. Des modèles de régression multiple introduisant le chevauchement de la préférence de température et de profondeur et l'abondance des espèces comme variables indépendantes, représentaient une forte proportion de la variance totale dans la partie transformée des traits de chalut dans lesquels on retrouvait la présence simultanée d'espèces (R^2 moyen = 0,69 pour les poissons d'âge 1+, R^2 moyen = 0,44 pour les poissons d'âge 0). Les résultats montrent que même si la fréquence des interactions technologiques (prises accessoires) entre des paires d'espèces peut être très variable selon la saison, la zone et l'année, la présence simultanée entre les espèces est néanmoins assez prévisible. La minimisation des répercussions néfastes potentielles de la récolte d'espèces mélangées (c.-à-d. l'incapacité d'atteindre les objectifs de gestion pour toutes les espèces simultanément) peut être réalisée par l'exploitation de chacun des stocks pendant des périodes de séparation spatiale maximale et par l'utilisation des données sur les déterminants de la co-répartition de l'espèce afin de prévoir avec plus de précision le niveau des prises accessoires.

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Mixed-species harvesting has been termed technological interaction: the exploitation of species "mixtures" by fishing technology (gear) that is deployed so as to capture species/stocks indiscriminately (Pope 1979; Murawski et al. 1983; Mahon 1985a; Shepherd 1988). The implications of technological interactions to the achievement of species-specific management goals are clear. It may not be feasible to affect a suite of species goals simultaneously, given joint harvest, particularly if the relative status of various stocks comprising the mixture is significantly different. Numerous studies have eval-

uated the feasibility of achieving single species catch quotas (Brown et al. 1979; Overholtz 1985; Sinclair 1985) or fishing mortality rates (Murawski and Finn 1986) for the various species components of a mixed resource. Similarly, methods have been developed with which to evaluate a "global" optimal harvest policy, given the inherent trade-offs necesssary in the management of such mixtures (Hilborn 1976; Murawski 1984; Brander and Bennett 1986; Shepherd 1988).

Despite the recent attention directed to the study of technological interactions as operational impediments to effective management, basic processes responsible for the joint occurrence of two or more stocks remain poorly understood. It is well known, for example, that the distribution of demersal fish fauna is correlated with depth and temperature (e.g. Gabriel and Tyler 1980; Overholtz and Tyler 1985; Mahon 1985b). Yet, these and other environmental variables tend to be collinear, and statistical models of species abundance against these gradients tend to explain a small proportion of the overall variance in site-specific abundance (Overholtz and Tyler 1985).

In this study we analyze the environmental determinants of fish distributions for a multispecies demersal fauna on Georges Bank in the Northwest Atlantic and relate the site-specific co-distribution of species to multidimensional overlaps in environmental preferences. Further, an evaluation of the effects of species abundance on the spatial distribution of species is presented, particularly as related to changes in the frequency of co-occurrence with other species. Finally, a statistical description of the relationship among abiotic (i.e. oceanographic) and biotic (species abundance) variables and the frequency of site-specific co-occurrence is evaluated as an empirical model for describing general processes underlying technological interactions.

Approach and Data

A fundamental question implied in technological interactions (harvesting of co-occurring species) is that of the spatial scale at which mixed-species harvesting gears are deployed, in relation to the small-scale distribution patterns of the species sought. It is doubtful that species actually co-exist on a very localized scale as true mixtures. Rather, small patches of schooling fishes of a species may randomly encounter similar patches of other highly mobile fishes and swim over aggregations of benthic species (e.g. flounders, angler fishes). Deployment of a mobile, species-indiscriminant fishing gear, such as an otter trawl, will act to integrate various patches of these species into an aggregate mixed-species catch (sample). If an individual set of the gear is fished over a long transect (e.g. time of tow is great), or if the gear integrates across an important environmental gradient (e.g. a wide depth range), the aggregate catch may not resemble the actual distribution patterns of the species involved. A common reaction of otter trawl fleets, particularly as resources decline in abundance, is that average time of tow increases. Such a situation results in the integration of even more "patches" of different species, thereby exacerbating the "bycatch" nature of the fishery.

Little, if any, data exist with which to estimate the local-scale density distribution of marine fishes, particularly with respect to coincident bottom trawl sampling. Commercial otter trawl tow-by-tow data are usually not available for estimating species compositions at discrete times and places. Furthermore, because of the long tow times commonly exhibited in these fisheries (1–3 h at 3–4 kn), commercial catch data may be too crude a tool with which to evaluate biological/physical processes associated with "coincident" species distributions. Also, the only physical variables generally available from dockside sampling data are possibly imprecise positions for the tows generating the landings, and an average water depth. Given these considerations, we chose to analyze patterns in species co-distribution based on standardized bottom trawl survey time series data.

Data used in these analyses are from the time-series of research vessel bottom trawl surveys of northwest Atlantic waters, conducted by the Northeast Fisheries Center (NEFC), National Marine Fisheries Service (NMFS). Survey procedures, equipment, and data processing have been reviewed by Grosslein (1969) and Azarovitz (1981). Briefly, routine surveys are conducted in continental shelf waters from southern Nova Scotia to southern North Carolina. A stratified-random sampling scheme is employed, with the number of stations occupied generally proportional to the area of individual strata. Stratum boundaries are based primarily on depths and, to a lesser extent, bottom type. Survey strata in the Georges Bank region are illustrated in Fig. 1. Depth ranges and associated stratum areas (weighting coefficients) are given in Table 1.

At each randomly determined sampling location, a 30-min bottom trawl tow was conducted. Each tow sampled a swath of approximately 1.5-1.75 nautical miles, as the tow speed was approximately 3.5 kn. Because stations were randomly selected within depth strata, the variation in water depth within individual tows is generally small. All finfish and invertebrate species caught were enumerated and weighed, and subsamples were measured for size frequency distributions. An expendable bathythermograph cast was made at each station to determine temperature profiles. Autumn–winter surveys have been conducted annually since 1963 (Table 2), and spring surveys since 1968. Summer surveys have been made intermittently. The number of stations occupied during each Georges Bank survey remained relatively stable during 1963–76, increased markedly during 1977–80, and has since declined. All winter, summer, and autumn surveys have been conducted utilizing a 36-Yankee otter trawl (Azarovitz 1981). Spring surveys during 1973–81 employed a larger 41-Yankee trawl. This larger trawl was used to increase the precision and accuracy of abundance indices for various stocks.

A total of 4028 bottom trawl survey tows were conducted in the Georges Bank region during 44 cruises conducted from 1963 to 1981 (Table 2). Data from autumn surveys during 1982–86 (509 trawl tows) were reserved for model testing and validation. Of the total tows conducted during 1963–81, 6% were during winter, 32% in spring, 14% in summer, and 47% in autumn surveys. One hundred and sixty (160) of the tow records lacked bottom water temperature data and were excluded from analysis.

Our initial task was to describe the distribution of seven of the most important groundfish species, based on season of capture, depth, and bottom water temperature (Fig. 1; Table 1): Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), pollock (*Pollachius virens*), yellowtail flounder (*Limanda ferruginea*), winter flounder (*Pseudopleuronectes americanus*), silver hake (*Merluccius bilinearis*), and red hake (*Urophycis chuss*). These species comprise the bulk of the commercial Georges Bank landings and account for a significant portion of the total demersal finfish biomass (Clark and Brown 1977; Overholtz 1982). Because the survey sampling is based on a stratified random scheme, it is in theory possible to regroup the survey data on each of the above variables (season, depth, temperature) without serious statistical bias. Accordingly, all

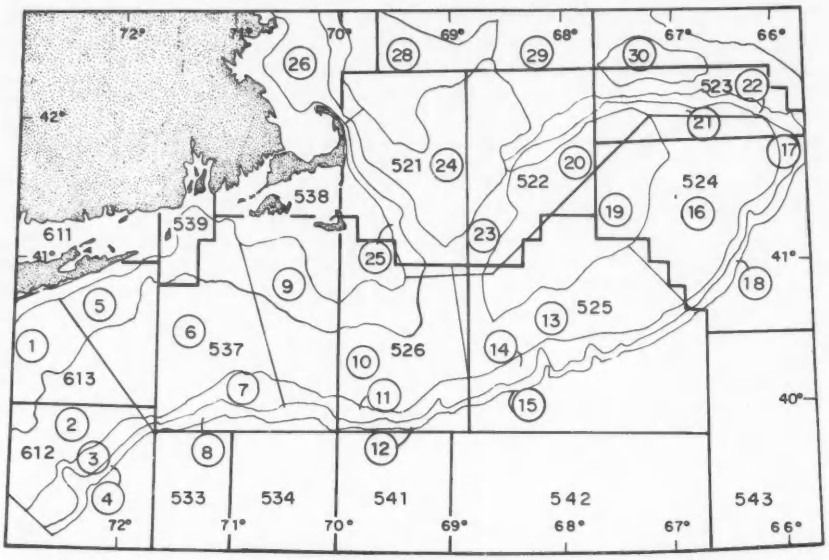

FIG. 1. Statistical reporting areas (three digits) in the Georges Bank region, with NMFS bottom trawl survey strata (two digits in circles) superimposed. Stratum areas and depth ranges are given in Table 1.

TABLE 1. Area, depth range, and overlap with statistical reporting areas of NMFS bottom trawl survey strata in the Georges Bank region. Stratum boundaries are given in Fig. 1.

Stratum No.[b]	Area (square nautical miles)	Depth range		Associated statistical areas[a]					
		Fathoms	Metres	521	522	523	524	525	526
9 (*P*)	1522	15–30	27–55						×
10 (*P*)	2722	31–60	56–110						×
11 (*P*)	622	61–100	111–183						×
12 (*P*)	176	>100	>183						×
13	2374	31–60	56–110					×	
14	656	61–100	111–183					×	
15	230	>100	>183					×	
16	2980	31–60	56–110			×	×	×	
17	360	61–100	111–183			×	×		
18	172	>100	>183			×	×		
19	2454	15–30	27–55			×	×	×	
20	1221	15–30	27–55		×	×	×	×	
21	424	31–60	56–110			×			
22 (*P*)	454	61–100	111–183			×			
23	1016	31–60	56–110	×	×			×	×
24 (*P*)	2569	61–100	111–183	×	×				
25	390	15–30	27–55	×					×
26 (*P*)	1014	31–60	56–110	×					
27 (*P*)	720	61–100	111–183	×					
28 (*P*)	2249	>100	>183	×	×				
29 (*P*)	3245	>100	>183		×	×			
30 (*P*)	619	>100	>183			×			

[a]Statistical reporting areas (Fig. 1) that overlap the survey strata are indicated by ×.

[b]Only a portion of the strata indicated by a (*P*) are included in the Georges Bank region.

survey data were grouped by season and sequentially poststratified by 10-m depth interval and 1°C bottom temperature. Survey tows falling outside statistical areas 521–526 (Table 1; Fig. 1) were deleted from further analysis. Data were analyzed separately for age 0 and age 1 and older animals for each of the seven species. Age 0 animals are defined as those not having completed one *biological* year of life (i.e. ageing is not incremented with the calendar year). The number of fish caught at each tow in each species/age group was determined based on length frequency cutpoints to separate the two age groups

TABLE 2. Research vessel bottom trawl surveys of the Georges Bank area used for the analysis of co-distribution of seven demersal fish species, 1963–86.

Year	Season	Sampling dates[a] (d/mo – d/mo)	No. of stations occupied[a]
1963	Summer	26/7–14/8	77
	Autumn	15/11–9/12	75
1964	Winter	18/1–10/2	79
	Autumn	23/10–24/11	44
1965	Winter	2/2–8/4	87
	Summer	7/7–10/8	83
	Autumn	10/10–9/11	93
1966	Winter	21/1–23/2	87
	Autumn	12/10–10/11	88
1967	Autumn	17/10–9/12	93
1968	Spring	16/3–13/5	87
	Autumn	20/10–20/11	87
1969	Spring	19/3–10/4	96
	Summer	10/4–21/8	86
	Autumn	27/10–23/11	94
1970	Spring	12/3–19/4	85
	Autumn	23/10–8/11	88
1971	Spring	13/3–19/4	92
	Autumn	15/10–6/11	92
1972	Spring	28/3–24/4	98
	Autumn	10/10–4/11	95
1973	Spring[b]	9/3–22/3	87
	Autumn	9/10–5/11	88
1974	Spring[b]	3/3–28/3	81
	Autumn	5/10–21/10	91
1975	Spring[b]	22/3–6/5	85
	Autumn	8/10–7/11	97
1976	Spring[b]	27/3–18/4	92
	Autumn	23/10–21/11	82
1977	Spring[b]	18/4–2/5	88
	Summer	3/8–31/8	72
	Autumn	19/10–15/12	124
1978	Spring[b]	5/4–24/5	97
	Summer	6/8–19/8	64
	Autumn	30/9–20/11	182
1979	Spring[b]	31/3–12/5	130
	Summer	8/8–20/8	66
	Autumn	13/10–18/11	187
1980	Spring[b]	10/4–1/5	98
	Summer	30/7–31/8	65
	Autumn	12/10–14/11	115
1981	Spring[b]	15/4–22/5	85
	Summer	11/7–23/7	53
	Autumn	13/10–7/11	94
1982	Autumn[c]	12/10–11/11	112
1983	Autumn[c]	8/10–9/11	128
1984	Autumn[c]	8/10–25/10	94
1985	Autumn[c]	17/10–13/11	91
1986	Autumn[c]	7/10–30/10	84

[a]Dates and numbers of stations sampled in the Georges Bank portion of the survey.

[b]Spring surveys employed a larger trawl during 1973–81 (Azarovitz 1981).

[c]Data from autumn surveys during 1982–86 used to validate regression models only.

(Bowman 1981). A second data base was thus created, listing for each tow the date, cruise, depth, bottom temperature, and catch in numbers for the two age groups of each of the seven species analyzed. These are the basic data used, then, to analyze patterns in species distribution and co-occurrence.

Environmental Determinants of Species Distribution

Environmental data were used in conjunction with abundance (numbers) information to compute weighted mean and standard deviations of depth and temperature at capture for each species/age:

$$\text{Mean} = \frac{\Sigma (f_i x_i)}{\Sigma f_i}$$

$$\text{Standard deviation} = \text{SQRT}\,[(\Sigma(f_i x_i^2)) - ((\Sigma f_i)\text{mean}^2) \div (\Sigma f_i) - 1]$$

where f_i = numbers of fish taken in tow i and x_i = depth (or temperature) at tow i. Results of these computations are presented in Table 3. Data are given by season and are based on survey tows conducted during 1963–81 (Table 2). Scattergrams of seasonal temperature at depth (Fig. 2 and 3) were used in conjuction with mean temperatures and depths at capture to examine patterns in distribution of individual species/ages in relation to the range of available temperatures/depths (i.e. Fig. 4).

During winter and spring surveys (January through early May), shallow waters were generally cooler than deeper areas; the reverse was true for summer and autumn surveys (July through early December; Fig. 2). Greatest variability in annual bottom water temperatures occurred at depths less than about 200 m. Little annual temperature variation occurred at depths beyond 250 m. Waters less than 100 m were subject to temperatures between 1 and 17°C; in waters greater than 250 m, temperatures ranged between 5 and 12°C (Fig. 3).

Seasonal changes in mean depth/temperature at capture ranged from slight changes in depth by season (e.g. winter and yellowtail flounders), with corresponding large variation in seasonal temperature at capture, to modest changes in temperature at capture (e.g. silver hake 1+), with a substantial change in seasonal depth at capture (Table 3). The species/ages analyzed herein can generally be classified relative to their stability in temperature and depth preferences throughout the year. Some either maintain near-constant depths, and therefore undergo wide variation in annual temperature (e.g. yellowtail, winter flounder), or seek a relatively narrow preferred temperature range, and therefore moves spatially to find these preferred temperatures (e.g. silver and red hakes). Coefficients of variation (CV = SD/mean) of weighted depths at capture for particular seasons (Table 3) are in virtually all cases greater than corresponding CV's of temperatures at capture by species/age and season. However, within particular species/age groups, the CV's of seasonal mean depths and temperatures at capture are highly variable, depending on the environmental cue most important (Fig. 5). For example, the CV of mean seasonal depth for silver hake age 1+ is 0.29, with a corresponding CV of temperature = 0.17 (apparently seeking a relatively stable thermal regime). By contrast, the CV of mean depth for winter flounder age 1+ is 0.05, with a CV in temperature = 0.54 (Table 3). Only two of the species exhibited CV's in depth greater than in temperature (silver and red hakes; Fig. 5). In all cases, age 0 fish were characterized by more variability in tem-

TABLE 3. Mean, standard deviation (SD), and coefficient of variation (CV = SD/mean) of depth and temperature at capture of seven demersal fish stocks in the Georges Bank region during NMFS bottom trawl surveys, 1963–81. Data are given for two age groups (ages 1+ and 0) by season (1 = winter, 2 = spring, 3 = summer, 4 = autumn). Catches are weighted by numbers per tow.

Species/age	Season	Mean depth	SD depth	CV depth	Mean temp.	SD temp.	CV temp.
Silver hake 1+	1	208.00	40.49	0.19	5.97	0.89	0.15
	2	185.96	71.88	0.39	8.45	2.35	0.28
	3	96.95	52.05	0.54	8.95	2.66	0.30
	4	162.78	66.24	0.41	8.42	2.47	0.29
Silver hake 0	1	125.77	61.81	0.49	5.15	0.71	0.14
	2	159.78	60.93	0.38	6.19	1.21	0.20
	3	104.76	55.71	0.53	8.17	2.51	0.31
	4	74.47	38.97	0.52	12.60	2.54	0.20
Atlantic cod 1+	1	87.68	53.01	0.60	4.24	1.09	0.26
	2	67.17	30.28	0.45	5.39	0.86	0.16
	3	72.38	33.45	0.46	8.06	1.97	0.24
	4	84.45	44.42	0.53	9.31	2.43	0.26
Atlantic cod 0	1	56.13	10.73	0.19	2.95	0.21	0.07
	2	60.39	19.74	0.33	5.27	0.79	0.15
	3	70.93	17.40	0.25	9.92	2.77	0.28
	4	70.59	28.19	0.40	9.37	2.13	0.23
Haddock 1+	1	115.34	48.13	0.42	4.50	1.16	0.26
	2	79.41	24.98	0.31	5.54	0.99	0.18
	3	79.94	38.27	0.48	9.45	2.07	0.22
	4	107.99	46.68	0.43	8.82	2.24	0.25
Haddock 0	1	99.61	24.75	0.25	4.71	0.65	0.14
	2	84.30	21.16	0.25	5.40	0.89	0.16
	3	73.83	27.83	0.38	10.95	2.57	0.23
	4	73.66	29.24	0.40	10.12	2.75	0.27
Pollock 1+	1	132.37	57.02	0.43	4.83	1.46	0.30
	2	105.58	51.06	0.48	5.53	1.45	0.26
	3	108.72	50.77	0.47	6.78	1.70	0.25
	4	136.19	43.00	0.32	7.52	1.27	0.17
Pollock 0	1	0.00	0.00	0.00	0.00	0.00	0.00
	2	73.40	45.28	0.62	4.37	0.84	0.19
	3	191.00	0.00	0.00	8.20	0.00	0.00
	4	69.40	37.90	0.55	11.54	0.99	0.09
Red hake 1+	1	164.78	35.47	0.22	5.71	0.71	0.12
	2	150.87	63.29	0.42	7.10	2.41	0.34
	3	85.65	29.51	0.34	8.81	2.04	0.23
	4	111.63	50.15	0.45	9.92	2.37	0.24
Red hake 0	1	128.64	28.54	0.22	5.03	0.31	0.06
	2	119.53	58.81	0.49	5.66	1.62	0.29
	3	70.34	28.75	0.41	10.30	2.09	0.20
	4	71.60	31.95	0.45	12.81	1.97	0.15
Yellowtail flounder 1+	1	69.91	33.60	0.48	3.65	1.10	0.30
	2	72.58	21.01	0.29	5.22	1.57	0.30
	3	66.09	16.40	0.25	9.93	1.91	0.19
	4	68.08	22.38	0.33	11.01	2.08	0.19
Yellowtail flounder 0	1	56.05	14.44	0.26	3.14	1.29	0.41
	2	63.87	15.11	0.24	4.67	0.91	0.20
	3	73.75	39.26	0.53	9.70	3.85	0.40
	4	87.28	26.15	0.30	8.84	2.46	0.28
Winter flounder 1+	1	49.63	15.59	0.31	3.23	0.71	0.22
	2	56.09	17.25	0.31	5.05	0.96	0.19
	3	52.19	17.19	0.33	10.75	2.82	0.26
	4	52.26	14.94	0.29	11.72	1.98	0.17
Winter flounder 0	1	53.00	0.00	0.00	4.00	0.00	0.00
	2	43.98	10.10	0.23	5.34	0.71	0.13
	3	52.14	13.26	0.25	13.69	1.69	0.12
	4	47.31	9.86	0.21	11.34	1.73	0.15

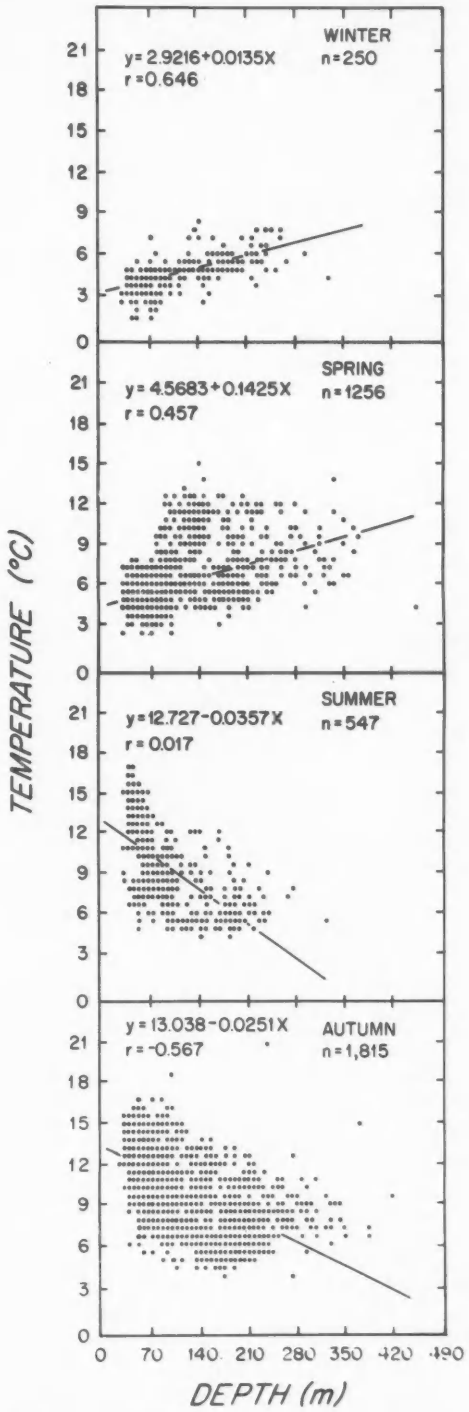

FIG. 2. Seasonal relationships between bottom water temperature and depth in the Georges Bank region, 1963–81. Data were obtained during bottom trawl surveys described in Table 2.

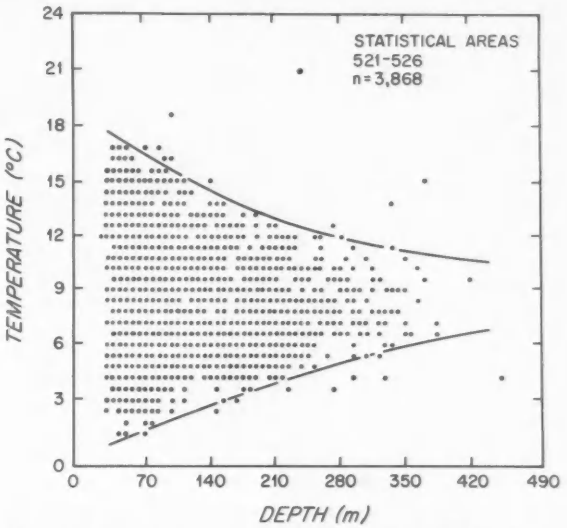

FIG. 3. Variability in bottom water temperature at depth in the Georges Bank region, 1963–81. Data were obtained during bottom trawl surveys described in Table 2 and are for all seasons combined. Lines indicate the approximate minimum and maximum temperatures at depth.

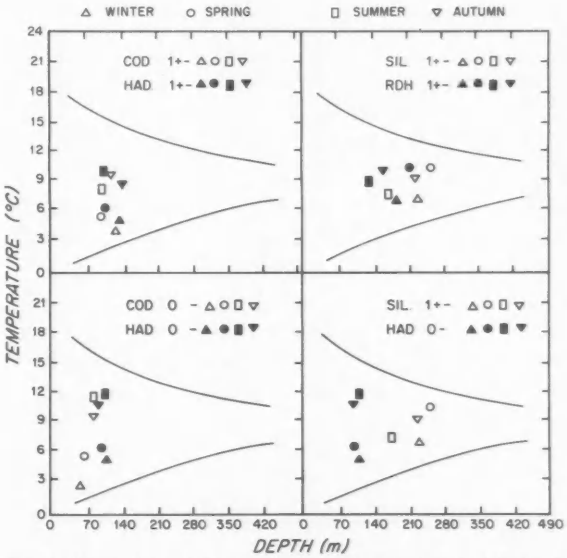

FIG. 4. Comparison of the seasonal mean temperature and depth of occurrence of selected pairs of demersal fish species in the Georges Bank region. Lines are the approximate minimum and maximum temperatures at depth. Data are separated by age group for each species (age 1+, 0) and are from NMFS bottom trawl surveys, 1963–81.

perature than in depth. This is primarily due to the generally shallower distributions of age 0 fish than age 1+ within a species (Table 3). None of the species we considered exhibited high CV's in annual depth at capture, with correspondingly low CV's in temperature (lower right corner of Fig. 5). However, two pelagic stocks, longfin squid, (*Loligo pealei*), and butterfish (*Peprilus triacanthus*), in the mid-Atlantic region, south of

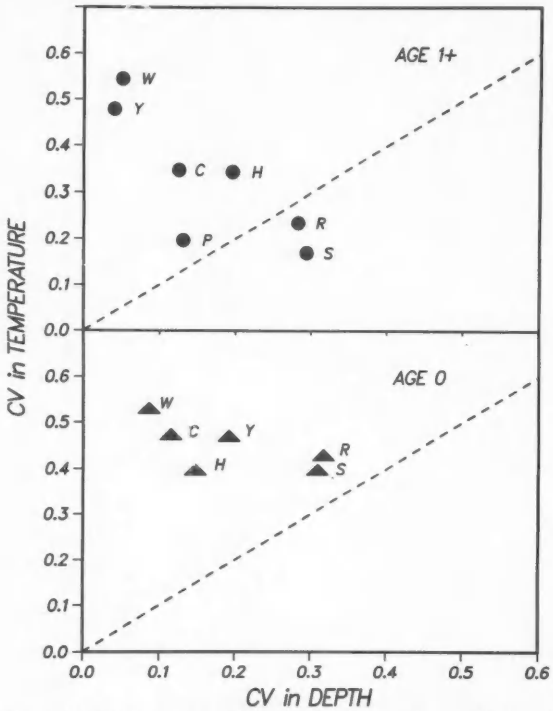

FIG. 5. Coefficients of variation (CV) in seasonal mean depth and temperature at capture (Table 3) for seven demersal fish species on Georges Bank (S = silver hake, C = Atlantic cod, H = haddock, P = pollock, R = red hake, Y = yellowtail flounder, W = winter flounder). Data are plotted for age 1+ and age 0 separately. Broken lines represent equal CVs.

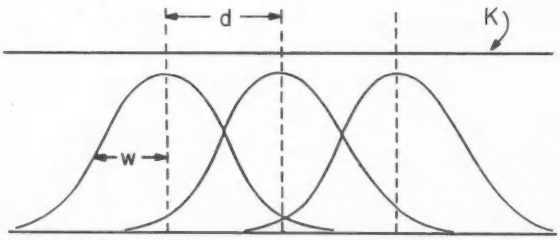

FIG. 6. Overlap along a resource continuum (K) of resource utilization by several species. K may represent temperature, depth, etc. The value d represents the distance between means for a pair of species and w is the standard deviation of the resource utilization curve for a species. (From May 1973)

Georges Bank, show such patterns. The CV's in depth of squid and butterfish were 0.72 and 0.55, respectively, with CV's in temperature of 0.13 and 0.17.

The classification scheme based on variability in annual temperature and depth at capture may be useful in determining those species and age groups likely to exhibit significant variation in availability to fisheries. Given the temperature affinities of squid, butterfish, and hakes, these species would be expected to exhibit substantially greater fluctuation in catchability and availability to fisheries at specific geographic locations and times than would species such as winter and yellowtail flounders.

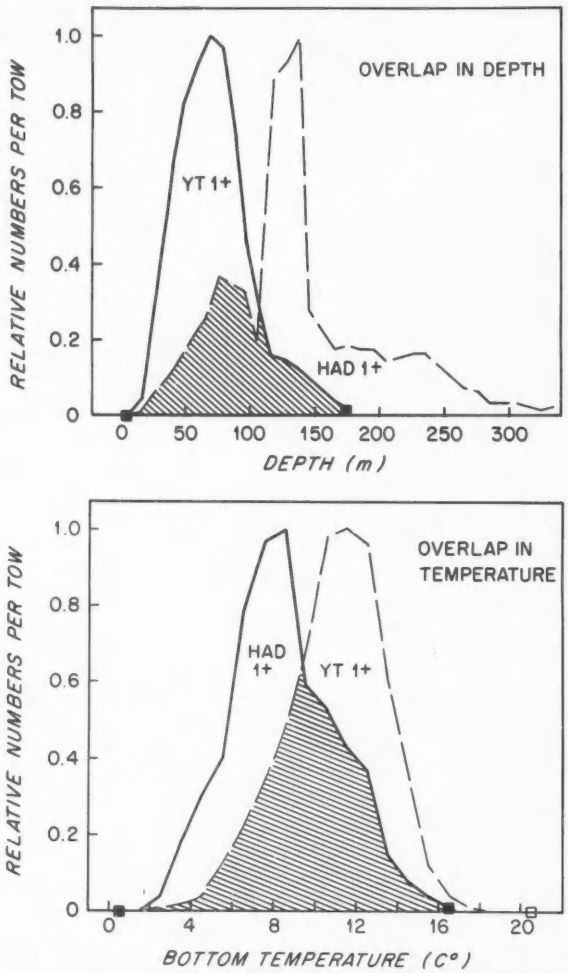

FIG. 7. Relative abundance of Georges Bank haddock and yellowtail flounder by depth and bottom temperature for autumn bottom trawl surveys, 1963–81. Data are mean numbers per tow in depth and temperature intervals, standardized to the maximum value. A moving three-point average was employed to smooth the data. Shaded area is the zone of overlap in depth/temperature preferences. Because of the inverse relationship between depth and temperature in autumn surveys (Fig. 2), yellowtail flounder are distributed in shallower, warmer waters than haddock.

Overlap in seasonal temperature/depth preferences among the various species/ages was computed in the following manner. The distribution of a species along environmental continua can be approximated by a normal distribution (Fig. 6 and 7; May 1973). The intersection of these normal distributions (Fig. 6) is described by

$$\mathrm{ALPHA}_{ij} = C_{ij} \exp\left[-d^2/2(w_i^2 + w_j^2)\right]$$
$$C_{ij} = (2w_i w_j/(w_i^2 + w_j^2))^{1/2}$$

where ALPHA_{ij} = overlap coefficient between species/ages i and j, d = "distance" between mean environmental values for species i and j (Fig. 6), and w_i, w_j = standard deviations of the resource utilizations of species/ages i and j along an environmental continuum (May 1973). Coefficients of overlap

TABLE 4. Coefficients of overlap in environmental preferences between pairs of demersal fish species in the Georges Bank region. Data are for overlap in depth preferences and are based NMFS bottom trawl sampling from 1963–81. Data are presented for the four seasons (sea, 1 = winter, 2 = spring, 3 = summer, 4 = autumn). S = silver hake, C = Atlantic cod, H = haddock, P = pollock, R = red hake, Y = yellowtail flounder, W = winter flounder.

Species/age	Sea	S 1+	S 0	C 1+	C 0	H 1+	H 0	P 1+	P 0	R 1+	R 0	Y 1+	Y 0	W 1+	W 0
S 1+	1	1.00													
	2	1.00													
	3	1.00													
	4	1.00													
S 0	1	0.52	1.00												
	2	0.96	1.00												
	3	0.99	1.00												
	4	0.48	1.00												
C 1+	1	0.19	0.89	1.00											
	2	0.27	0.35	1.00											
	3	0.88	0.83	1.00											
	4	0.59	0.98	1.00											
C 0	1	0.00	0.31	0.53	1.00										
	2	0.17	0.23	0.94	1.00										
	3	0.69	0.64	0.90	1.00										
	4	0.37	0.97	0.92	1.00										
H 1+	1	0.34	0.98	0.93	0.32	1.00									
	2	0.30	0.40	0.94	0.83	1.00									
	3	0.94	0.90	0.99	0.85	1.00									
	4	0.77	0.85	0.93	0.74	1.00									
H 0	1	0.07	0.77	0.86	0.23	0.86	1.00								
	2	0.29	0.40	0.87	0.71	0.98	1.00								
	3	0.84	0.79	0.99	0.94	0.97	1.00								
	4	0.40	0.98	0.94	1.00	0.78	1.00								
P 1+	1	0.54	1.00	0.85	0.25	0.97	0.74	1.00							
	2	0.64	0.78	0.76	0.58	0.80	0.78	1.00							
	3	0.99	1.00	0.80	0.61	0.88	0.77	1.00							
	4	0.90	0.57	0.70	0.42	0.90	0.47	1.00							
P 0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00						
	2	0.39	0.51	0.96	0.83	0.91	0.86	0.89	1.00						
	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00						
	4	0.44	1.00	0.96	0.98	0.81	0.98	0.51	1.00						
R 1+	1	0.72	0.80	0.46	0.01	0.69	0.31	0.84	0.00	1.00					
	2	0.93	0.99	0.43	0.30	0.48	0.47	0.85	0.59	1.00					
	3	0.91	0.87	0.95	0.85	0.98	0.96	0.86	0.00	1.00					
	4	0.81	0.83	0.92	0.72	1.00	0.75	0.93	0.78	1.00					
R 0	1	0.27	0.87	0.72	0.05	0.91	0.74	0.89	0.00	0.72	1.00				
	2	0.77	0.89	0.66	0.49	0.70	0.68	0.98	0.81	0.94	1.00				
	3	0.83	0.78	0.99	0.94	0.96	1.00	0.75	0.00	0.93	1.00				
	4	0.41	0.99	0.95	1.00	0.79	1.00	0.47	0.99	0.76	1.00				
Y 1+	1	0.03	0.67	0.91	0.71	0.72	0.76	0.60	0.00	0.15	0.41	1.00			
	2	0.23	0.31	0.96	0.91	0.97	0.93	0.70	0.87	0.39	0.60	1.00			
	3	0.65	0.59	0.88	0.98	0.81	0.91	0.56	0.00	0.78	0.92	1.00			
	4	0.31	0.92	0.85	0.98	0.66	0.97	0.34	0.94	0.63	0.97	1.00			
Y 0	1	0.00	0.36	0.60	0.98	0.37	0.29	0.30	0.00	0.01	0.06	0.79	1.00		
	2	0.16	0.21	0.89	0.97	0.82	0.71	0.54	0.76	0.27	0.46	0.92	1.00		
	3	0.92	0.88	0.99	0.86	0.99	0.97	0.85	0.00	0.95	0.97	0.83	1.00		
	4	0.47	0.93	0.93	0.91	0.86	0.94	0.59	0.90	0.83	0.92	0.85	1.00		
W 1+	1	0.00	0.34	0.58	0.91	0.33	0.22	0.27	0.01	0.00	0.05	0.75	0.95	1.00	
	2	0.14	0.19	0.88	0.98	0.72	0.58	0.51	0.77	0.25	0.43	0.82	0.94	1.00	
	3	0.55	0.50	0.78	0.75	0.69	0.76	0.45	0.00	0.58	0.81	0.84	0.76	1.00	
	4	0.17	0.71	0.61	0.77	0.40	0.73	0.14	0.76	0.39	0.75	0.81	0.47	1.00	
W 0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.08	0.10	0.60	0.68	0.35	0.20	0.31	0.53	0.14	0.26	0.42	0.53	0.78	1.00
	3	0.49	0.44	0.71	0.68	0.62	0.69	0.39	0.00	0.51	0.74	0.79	0.68	0.98	1.00
	4	0.12	0.55	0.47	0.58	0.28	0.54	0.09	0.60	0.28	0.58	0.60	0.29	0.92	1.00

TABLE 5. Coefficients of overlap in environmental preferences between pairs of demersal fish species in the Georges Bank region. Data are for overlap in bottom water temperature preferences and are based on NMFS bottom trawl sampling from 1963–81. Data are presented for the four seasons (sea, 1 = winter, 2 = spring, 3 = summer, 4 = autumn). S = silver hake, C = Atlantic cod, H = haddock, P = pollock, R = red hake, Y = yellowtail flounder, W = winter flounder.

Species/age	Sea	S 1+	S 0	C 1+	C 0	H 1+	H 0	P 1+	P 0	R 1+	R 0	Y 1+	Y 0	W 1+	W 0
S 1+	1	1.00													
	2	1.00													
	3	1.00													
	4	1.00													
S 0	1	0.76	1.00												
	2	0.63	1.00												
	3	0.98	1.00												
	4	0.50	1.00												
C 1+	1	0.46	0.75	1.00											
	2	0.38	0.84	1.00											
	3	0.94	0.99	1.00											
	4	0.97	0.65	1.00											
C 0	1	0.00	0.01	0.31	1.00										
	2	0.34	0.78	0.99	1.00										
	3	0.97	0.89	0.84	1.00										
	4	0.95	0.62	1.00	1.00										
H 1+	1	0.59	0.84	0.99	0.25	1.00									
	2	0.44	0.91	0.99	0.97	1.00									
	3	0.97	0.92	0.88	0.97	1.00									
	4	0.99	0.53	0.99	0.98	1.00									
H 0	1	0.50	0.90	0.88	0.02	0.91	1.00								
	2	0.39	0.85	1.00	0.99	0.99	1.00								
	3	0.86	0.74	0.66	0.96	0.89	1.00								
	4	0.90	0.80	0.97	0.96	0.92	1.00								
P 1+	1	0.75	0.87	0.93	0.23	0.97	0.86	1.00							
	2	0.54	0.93	0.93	0.91	0.97	0.94	1.00							
	3	0.75	0.87	0.88	0.59	0.60	0.38	1.00							
	4	0.86	0.18	0.73	0.71	0.81	0.60	1.00							
P 0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00						
	2	0.21	0.45	0.70	0.74	0.66	0.70	0.73	1.00						
	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00						
	4	0.42	0.76	0.58	0.57	0.46	0.71	0.04	1.00						
R 1+	1	0.96	0.86	0.51	0.00	0.64	0.58	0.77	0.00	1.00					
	2	0.92	0.85	0.64	0.59	0.70	0.65	0.80	0.45	1.00					
	3	0.98	0.97	0.97	0.93	0.98	0.80	0.74	0.00	1.00					
	4	0.91	0.74	0.98	0.98	0.94	0.99	0.61	0.69	1.00					
R 0	1	0.48	0.84	0.57	0.00	0.64	0.79	0.63	0.00	0.59	1.00				
	2	0.60	0.95	0.90	0.87	0.94	0.91	1.00	0.70	0.85	1.00				
	3	0.91	0.80	0.74	0.97	0.96	0.97	0.42	0.00	0.88	1.00				
	4	0.38	0.98	0.53	0.49	0.41	0.71	0.07	0.76	0.64	1.00				
Y 1+	1	0.25	0.49	0.93	0.50	0.87	0.66	0.80	0.00	0.28	0.34	1.00			
	2	0.50	0.87	0.91	0.90	0.94	0.92	0.99	0.82	0.77	0.98	1.00			
	3	0.93	0.84	0.79	0.97	0.98	0.93	0.46	0.00	0.92	0.99	1.00			
	4	0.72	0.88	0.86	0.86	0.77	0.95	0.34	0.86	0.94	0.82	1.00			
Y 0	1	0.19	0.36	0.80	0.55	0.73	0.50	0.68	0.00	0.20	0.24	0.95	1.00		
	2	0.27	0.59	0.85	0.88	0.81	0.85	0.84	0.97	0.52	0.80	0.89	1.00		
	3	0.95	0.90	0.84	0.97	0.91	0.93	0.68	0.00	0.89	0.91	0.89	1.00		
	4	0.99	0.57	0.99	0.98	1.00	0.94	0.81	0.50	0.95	0.45	0.79	1.00		
W 1+	1	0.05	0.16	0.71	0.68	0.61	0.30	0.54	0.00	0.05	0.06	0.91	0.92	1.00	
	2	0.34	0.75	0.96	0.98	0.94	0.96	0.92	0.86	0.61	0.89	0.94	0.96	1.00	
	3	0.90	0.79	0.71	0.98	0.91	1.00	0.45	0.00	0.83	0.97	0.94	0.75	1.00	
	4	0.57	0.95	0.74	0.72	0.62	0.87	0.19	0.89	0.84	0.92	0.97	0.65	1.00	
W 0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.33	0.78	0.99	1.00	0.96	0.98	0.88	0.67	0.58	0.84	0.87	0.83	0.95	1.00
	3	0.31	0.18	0.09	0.48	0.28	0.64	0.02	0.00	0.18	0.45	0.34	0.55	0.63	1.00
	4	0.61	0.89	0.77	0.76	0.66	0.89	0.20	0.92	0.87	0.85	0.98	0.69	0.99	1.00

TABLE 6. Regression parameters for linear relationships between mean distance ($\log_e$ km) from the centroid of the distribution of groundfish species on Georges Bank to each tow of catch >0 and annual abundance (numbers per tow, $\log_e [n+1]$) in autumn bottom trawl surveys, 1963–81.

Species/age	Intercept (a)	Slope (b)	R	R^2	Probability
Silver hake 1+	4.9765	−0.0058	−0.07	<0.01	0.80
0	4.8730	−0.0081	−0.09	0.01	0.78
Atlantic cod 1+	5.1232	−0.1023	−0.39	0.15	0.10
0	4.1593	1.5124	0.30	0.09	0.26
Haddock 1+	5.1491	−0.0422	−0.39	0.15	0.10
0	4.3389	0.2381	0.27	0.07	0.29
Pollock 1+	4.1904	0.6781	0.28	0.08	0.25
0	—	—	—	—	—
Red hake 1+	4.7964	0.0665	0.45	0.02	0.06
0	4.6257	0.1041	0.33	0.11	0.17
Yellowtail flounder 1+	5.0417	0.0388	−0.21	0.04	0.39
0	3.2261	2.3227	0.44	0.19	0.09
Winter flounder 1+	4.3848	0.2751	0.41	0.17	0.08
0	2.2034	4.0842	0.34	0.11	0.30

TABLE 7. Regression parameters for linear relationships between dispersion indices (DI = $(S^2/\text{mean} - 1)/n - 1$) and $\log_e$ (mean + 1) catch (number per tow) for seven demersal fish species taken in autumn NMFS bottom trawl surveys of the Georges Bank region, 1963–81. Data are presented for two age groups of each species (1+, 0).

Species/age	Intercept (a)	Slope (b)	R	R^2	Probability[a]
Silver hake 1+	−0.0932	0.0587	0.58	0.34	0.01
0	0.0986	0.0073	0.11	0.01	0.65
Atlantic cod 1+	0.0792	−0.0069	−0.12	0.01	0.63
0	0.1771	0.2776	0.27	0.07	0.27
Haddock 1+	0.0331	0.0369	0.39	0.15	0.10
0	0.0544	0.0601	0.18	<0.01	0.47
Pollock 1+	0.1199	0.2837	0.45	0.20	0.05
0	−0.0451	−40.8560	−0.52	0.27	0.02
Red hake 1+	0.0932	−0.0050	−0.12	0.01	0.63
0	0.2864	−0.0507	−0.31	0.09	0.21
Yellowtail flounder 1+	0.0062	0.0279	0.34	0.11	0.16
0	0.1485	0.2697	0.25	0.07	0.30
Winter flounder 1+	0.1402	0.0054	0.02	<0.01	0.93
0	0.1830	1.7034	0.47	0.22	0.04
All species/all ages	0.1509	−0.0102	−0.05	<0.01	0.46
All species/age 1+	0.1667	−0.0250	−0.18	0.03	0.04
All species/age 0	0.1447	0.0132	0.04	<0.01	0.64

[a]Significance of overall regression.

($ALPHA_{ij}$) range from 0 (no overlap between species) to 1 (complete intersection of curves). These coefficients were computed for depth and temperature overlap separately for all possible pairs of species/ages (Tables 4 and 5). These calculations are illustrated in Fig. 7. Relative autumn catch distributions for yellowtail and haddock are plotted by temperature and depth. Overlap coefficients corresponding to these data are 0.66 for depth (Table 4) and 0.77 for temperature (Table 5). The multinomial intersection in these two variables (assuming independence) is then $(0.66 \times 0.77) = 0.51$. A further graphic example of these data is given in Fig. 4. Seasonal patterns in temperature/depth preferences between four selected pairs of species/ages illustrate the relative "distance" between species/ages in seasonal temperature/depth space and thus the likelihood for co-occurrence. Ellipses drawn between seasonal mean temperature/depth preferences define the environmental envelope occupied by the stock. Intersections of the ellipses (accounting for associated variances) determine the propensity of species to co-occupy the same temperature/depth space.

Analysis of Species Co-occurrence

The co-occurrence of various species/ages was assessed using a criterion of presence/absence, rather than the relationship between the continuous variables of numbers per tow. Use of the presence/absence criterion was deemed the most applicable, due to the major differences in catchability among species/ages considered, to the research vessel trawl (Clark and Brown

TABLE 8. Regression parameters for linear relationships between proportion of autumn bottom trawl survey tows not containing a particular species/age (arcsin [SQRT (PZ)]) and the log$_e$ (mean + 1) catch (number per tow). Data are from NMFS autumn surveys, 1963–81.

Species/age	Intercept (a)	Slope (b)	R	R^2	Probability[a]
Silver hake 1+	0.7535	−0.0670	−0.55	0.30	0.01
0	1.0678	−0.0851	−0.69	0.48	<0.01
Atlantic cod 1+	1.0792	−0.1381	−0.71	0.50	<0.01
0	1.4002	−0.2509	−0.58	0.33	<0.01
Haddock 1+	1.0190	−0.0655	−0.54	0.29	0.02
0	1.3526	−0.1777	−0.89	0.80	<0.01
Pollock 1+	1.1863	−0.0235	−0.12	0.02	0.62
0	1.5695	−8.6052	−0.98	0.96	<0.01
Red hake 1+	1.0483	−0.1104	−0.76	0.58	<0.01
0	1.3060	0.1424	−0.85	0.73	<0.01
Yellowtail flounder 1+	1.1578	−0.1295	−0.81	0.66	<0.01
0	1.4560	−0.3111	−0.82	0.67	<0.01
Winter flounder 1+	1.1991	−0.1239	−0.68	0.46	<0.01
0	1.5028	−0.3209	−0.58	0.34	0.01
All species/all ages	1.3768	−0.2272	−0.88	0.77	<0.01
All species/age 1+	1.1768	−0.1577	−0.76	0.60	<0.01
All species/age 0	1.4402	−0.2183	−0.91	0.82	<0.01

[a]Significance of overall regression.

TABLE 9. Regression parameters for linear relationships between the proportion of NMFS bottom trawl survey tows in the Georges Bank region containing co-occurring species (arcsin [SQRT (P_{ij})]) vs. overlap coefficients for temperature × depth preferences between species (Tables 4 and 5). Data are for all seasons combined.

Species/age	Intercept (a)	Slope (b)	R	R^2	Probability[a]
Silver hake 1+	0.4774	0.3743	0.51	0.26	0.01
0	0.0954	0.4288	0.59	0.34	<0.01
Atlantic cod 1+	0.4073	0.5052	0.70	0.49	<0.01
0	0.2919	0.1597	0.21	0.04	0.39
Haddock 1+	0.3958	0.5042	0.72	0.51	<0.01
0	0.2031	0.2022	0.26	0.07	0.26
Pollock 1+	0.3881	0.7912	0.75	0.56	<0.01
0	−0.2956	1.3296	0.50	0.25	0.10
Red hake 1+	0.3469	0.6076	0.59	0.35	<0.01
0	−0.0009	0.6938	0.52	0.27	0.02
Yellowtail flounder 1+	0.4354	0.4931	0.56	0.31	<0.01
0	0.4057	−0.0293	−0.03	<0.01	0.91
Winter flounder 1+	0.3852	0.8368	0.74	0.54	<0.01
0	0.3292	0.1861	0.11	0.01	0.68
All species/age 1+	0.4300	0.5322	0.61	0.37	<0.01
All species/age 0	0.2255	0.2820	0.26	0.07	<0.01

[a]Significance of overall regression.

1977). This is particularly true for the age 0 fishes which, depending on the species, may be poorly represented in survey catches, relative to their absolute abundance. However, the presence/absence of the species/age at a particular trawl station is probably adequately represented by the binary datum. We computed a matrix of porportions of trawl survey tows containing co-occurring species/age groups by season and year. These proportions of co-occurring species/ages (P_{ij}) were conditional, based on the catch of species i. Thus, P_{ij}'s were the proportion of tows catching species/age i also containing species/age j. Because of this conditionality, the proportion of tows, for example, containing age 1+ silver hake in quarter 1 (winter) that also contained age 0 silver hake (0.41) is different from the proportion of tows containing age 0 silver hake that also had age 1+ silver hake in quarter 1 (0.74). These data are correlated with environmental overlap and species abundance information in subsequent sections.

Species Abundance and Spatial Dispersion

The relationship of species abundance to various indices of spatial dispersion (capacity of the stock to "spread out" in rela-

TABLE 10. Multiple regression parameters for linear relationships between annual proportions of autumn bottom trawl survey tows containing co-occurring species (arcsin [SQRT (P_{ij})]) vs. overlap coefficients for temperature × depth preferences between species (B_1; Tables 4 and 5) and $\log_e$ (mean + 1) catch per tow (numbers) of species i (B_2) and species j (B_3). Probability and P values indicate the significance of the overall regression and individual parameters, respectively.

Species/age	a	B_1	P	B_2	P	B_3	P	R	R^2	Probability
Silver hake 1+	0.1340	0.2093	0.00	−0.0093	0.53	0.2241	0.00	0.89	0.78	<0.01
0	0.2256	−0.1382	0.01	0.0188	0.17	0.2615	0.00	0.85	0.72	<0.01
Atlantic cod 1+	0.1922	0.0501	0.40	0.0125	0.61	0.2245	0.00	0.83	0.69	<0.01
0	−0.0097	0.3715	0.01	0.2488	0.05	0.2216	0.00	0.54	0.29	<0.01
Haddock 1+	−0.0499	0.3728	0.00	−0.0120	0.25	0.2259	0.00	0.84	0.71	<0.01
0	−0.0632	0.1620	0.08	0.0121	0.47	0.2668	0.00	0.73	0.53	<0.01
Pollock 1+	0.0583	0.5690	0.00	0.0255	0.54	0.2078	0.00	0.78	0.61	<0.01
0	−0.0822	0.0945	0.28	63.7909	0.00	0.0344	0.04	0.69	0.47	<0.01
Red hake 1+	0.1412	0.1191	0.07	−0.0264	0.14	0.2667	0.00	0.86	0.74	<0.01
0	0.2582	−0.0874	0.17	−0.0027	0.88	0.2949	0.00	0.81	0.66	<0.01
Yellowtail flounder 1+	0.2023	−0.0044	0.93	0.0074	0.75	0.2412	0.00	0.84	0.71	<0.01
0	0.1719	−0.0619	0.65	0.2427	0.02	0.2641	0.00	0.54	0.29	<0.01
Winter flounder 1+	0.3380	0.0219	0.72	−0.0627	0.16	0.2279	0.00	0.76	0.57	<0.01
0	−0.0410	0.5820	0.00	0.9092	0.00	0.1537	0.00	0.39	0.15	<0.01
All species/ages	0.0745	0.1619	0.00	0.0299	0.00	0.2260	0.00	0.61	0.37	<0.01
All species/age 1+	0.1503	0.1770	0.00	−0.0180	0.00	0.2387	0.00	0.81	0.65	<0.01
All species/age 0	0.0558	0.1669	0.00	0.0587	0.00	0.2134	0.00	0.50	0.25	<0.01

tion to changes in density) was evaluated from the series of autumn survey data (Table 2), since the time series has remained unbroken since 1963, with many of the stocks exhibiting substantial changes in abundance over that period (Clark and Brown 1977). Mean number per tow (nonstratified) was correlated with three alternative statistics used to describe the spatial distribution of the species/age groups.

An index of spatial dispersion was derived based on the average distance of animals sampled from the centroid of the species distribution. This involved computing the mean latitude and longitude from all positive catches of each species/age individually by year. These means are the unweighted centroids of the distributions of the animals. We reasoned that if a stock increases the area of distribution in relation to density, then the mean distance ($D_{i\cdot}$) from the centroid to all positive catches should also increase:

$$D_{i\cdot} = \frac{\sum_j DC_{ij}}{\sum_j} \quad \text{for } C_{ij} > 0$$

where $D_{i\cdot}$ = mean distance (kilometres) from the center of the distribution of species/age i to all positive tows, j, C_{ij} = catch (numbers) of species/age i in tow j, and DC_{ij} = distance (kilometres) from the center of the distribution of species/age i to the latitude and longitude of tow j, where $C_{ij} > 0$. Results of regressions of $\log_e D_{i\cdot}$ on abundance ($\log_e$[numbers per tow]) for autumn surveys conducted between 1963 and 1981 are given in Table 6. None of these regression equations was significant at the 5% level, indicating no apparent (either positive or negative) relationship between abundance and the average distance of animals from the geographic center of their distributions. These results may reflect the relatively narrow range of preferred environmental conditions exhibited by some of the species/ages, or the level of sampling intensity may not be sufficient to detect spatial dispersion changes of stocks with this statistic. Accordingly, two alternative dispersion indices were also computed and results compared with those above.

Green's index of spatial dispersion (Green 1986; Elliott 1977) was computed from annual abundance information from autumn surveys:

$$DI = (S^2/\text{mean}) - 1/n - 1$$

where DI = index of spatial dispersion, S^2 = variance of the number per tow, mean = mean number per tow, and n = numbers sampled (mean × number of tows). This particular index was chosen because it is one of a number of indices based on derivatives of the variance/mean ratio but appears relatively insensitive to the number of samples (tows), number of animals captured in all tows (n), and the sample mean. A simple variance/mean ratio is not adequate because of the obvious dependence of variance on mean (Elliott 1977). DI ranges from 1 when the stock exhibits maximum spatial contagion (i.e. all n are in one tow for a large n) to 0 for a random distribution and tends to $-(1/(n-1))$ for a distribution exhibiting maximum regularity.

Linear relationships between annual autumn abundance indices for the 14 species/ages and corresponding values of DI are summarized in Table 7. As with the distance to center computations (Table 6), relationships between DI and abundance were generally nonsignificant, i.e. the stocks do not appear to exhibit marked changes in spatial dispersion in relation to density flux.

The conclusion of a lack of relationship between density and spatial dipsersion is particularly important with respect to the adequacy of the presence/absence criterion as a measure of species co-occurrence. Generally, there were significant negative relationships between the proportion of tows not containing the species/age (PZ; proportion of zero tows) and abundance (Table 8). Co-occurrence as measured by a presence/absence criterion will be influenced by species abundances, but is not apparently a function of the stocks becoming more or less dispersed with density change. Rather, the increase in PZ with declining stock size probably reflects the expected increase in zero observations consistent with a negative binomial frequency

distribution (of research vessel survey catches), a low exponent, k, and a declining mean. This is illustrated for catch data of haddock age 1+. The overall frequency distribution of haddock catches is highly skewed, with a substantial fraction (57.5%) of zero tows. These data reflect years of high abundance, with correspondingly few zero tows (e.g. early 1960's), and vice versa. Parameters of the negative binomial frequency distribution were fitted viz.

$$P_{(x)} = [1+(u/k)]^{-k}\,[(k+x-1)!/x!(k-1)!]\,[u/(u+k)]^{x}$$

where $P_{(x)}$ = probability of x individuals in a tow, u = arithmetic mean of the catch per tow, and k = parameter of the negative binomial distribution. For $P_{(0)}$ the above equation simplies to

$$P_{(0)} = [1+(u/k)]^{-k}.$$

For the overall haddock catch data (1963–81), the estimated value of k is 0.103, with a mean catch per tow of 21.93. Substituting the k value and corresponding annual mean catches into the above equation results in annual estimates of the proportion of zero tows. The resulting estimates of the annual proportion of tows not containing age 1+ haddock (PZ) are generally close to empirical data. For example, in 1964, the mean catch per tow was the highest in the time series (79.27); the predicted PZ is 0.50 and the actual is 0.52. The lowest catch per tow occurred in 1971 (1.40) with a corresponding PZ value of 0.70. The aggregate negative binomial expansion estimate of PZ for 1971 is 0.76. These analyses illustrate that overall (multiyear) models may adequately describe the expected frequency of positive tows over a wide range of abundances. Thus, the change in observed PZ with stock size probably (for most species/ages) does not necessarily reflect a change in the spatial dispersion of the species but rather that which is consistent with an underlying negative binomial process.

Regressions of DI on log mean abundance are potentially confounded by the fact that some representation of the mean occurs in both the dependent and independent variables (although relationships between the two variables were generally not significant). To assess the potential sensitivity of our results to the choice of DI, we conducted a third set of analyses regressing annual estimates of $1/k$ (the parameter of the negative binomial distribution) on log abundance (Elliott 1977). Annual estimates of k were computed for each species/age group by iteratively solving

$$k_{jl} \log [1+(\text{mean}_{jl}/k)] = \log (1/\text{PZ}_{jl})$$

where mean_{jl} = annual mean catch per tow (numbers) for species/age l in year l, k_{jl} = negative binomial parameter k by species/age l and year l, and PZ_{jl} = proportion of zero tows of species/age j in year 1. Regressions of annual estimates of $1/k$ (an index of dispersion) on log abundance were not significant for any of the 14 species/ages investigated, although there was substantial variability in the computed slopes of the regression equations. These analyses further confirm our conclusions that indices of spatial dispersion are generally unrelated to species abundance, as measured by trawl survey monitoring results.

Statistical Models of Species Co-distribution

Regressions of the proportion of tows containing co-occurring species/ages versus overlap coefficients for temperature/depth preferences are given in Table 9. Most regressions were significant at the 1% level with a positive slope between environmental overlap coefficients and the proportion of co-occurrence between each pair of species/ages. However, even though these relationships were statistically significant, the amount of variance explained by them is generally not impressive (the best fits explain about half of the total variance). Thus, although there appears to be a clear effect of the overlap in environmental preferences in determining the propensity for species to co-occur, the signal contains substantial "noise." As noted above, an obvious source for the variability noted in the relationship is the effect of species abundance on the proportion of non-zero tows. As the proportion of zero tows is highly negatively correlated with abundance, it is clear that abundance data are an important covariate in a realistic model of factors influencing the probability of species co-occurrence. A series of multiple regression models with two abundance terms and accounting for environmental overlap were fitted utilizing autumn survey data for 1963–81:

$$\text{Arcsin}\,(\text{SQRT}[P_{ijl}]) = a + B_1(\text{ALPHA}_{ij}) + B_2[\log_e(\text{mean}_{il}+1)] + B_3[\log_e(\text{mean}_{jl}+1)] + e_{ijl}$$

where P_{ijl} = proportional co-occurrence of species i and j in year l, ALPHA_{ij} = overlap in temperature/depth preference between species, a,B = multiple regression parameters, and e_{ijl} = error term. Resulting multiple regression parameters for the various model fits are presented in Table 10. Data are summarized for each species/age combination separately and for all species/ages combined. In all cases the overall regressions are significant and explain substantially more of the total variance in species co-occurrence than linear regressions incorporating only environmental overlap as an independent variable (Table 9). The mean coefficients of determination for the single-species data in Table 10 were $R^2 = 0.69$ for age 1+ and $R^2 = 0.45$ for age 0. For most of the multiple regression models, patterns of residuals were consistent with adequate model fits. The exceptions were for species such as winter flounder age 0, where few individuals were caught on a particular survey. The parameter B_3 was significant at the 5% level in all multiple regression models and at the 1% level for all but one (Table 10). The parameter B_2, however, was only significant in a few cases, indicating that the effect of the first species in the regression was not an important explanatory variable. This is because of the conditional nature of the species co-occurrence data as specified. Proportional co-occurrence (between species/ages i and j) was measured conditional on tows containing the ith species. In eight of the multiple regression equations, the parameter accounting for environmental overlap (B_1) was not significant. Thus, depending on the species/age groups considered, the relative importance of abundance and environmental overlap coefficients in determining co-occurrence is quite variable.

Multiple regression equations were fitted to data for a particular species/age co-occurring with all 13 possible combinations. Regressions employing various subsets of these data (e.g. age 0 co-occurring only with age 0, etc.) would obviously be important in further defining the underlying ecological relationships among species. Nevertheless, aggregate regression models suggest the importance of both multidimensional overlap in environmental space and the abundance of individual species in determining the frequency at which seven species on Georges Bank will co-occur.

The adequacy of overall regression equations for predicting species co-occurrence was evaluated by comparing model per-

formance with autumn bottom trawl survey data from 1982–86 (years not used in developing the regression equations; Table 2). Relationships between observed and predicted transformed P_{ij}'s (based on multiple regression equations incorporating species abundance and environmental overlap; Table 10) were tested via linear correlation. Regressions of observed on predicted P_{ij} were forced through the origin and the slopes of the regressions tested against unity:

Species/age	Slope (b)	SE	R^2
Silver hake 1+	1.0314	0.0323	0.95
0	0.9412	0.0292	0.95
Cod 1+	1.0020	0.0298	0.95
0	0.9625	0.0595	0.85
Haddock 1+	1.0904	0.0366	0.95
0	1.3483	0.1143	0.77
Pollock 1+	1.0776	0.0493	0.92
0	0.5048	0.0706	0.88
Red hake 1+	1.0452	0.0370	0.94
0	0.9526	0.0389	0.92
Yellowtail flounder 1+	0.9252	0.0314	0.95
0	2.0704	0.2873	0.80
Winter flounder 1+	0.8169	0.0392	0.89
0	1.8958	0.1791	0.88
All species/ages	1.1151	0.0200	0.84
All species/age 1+	0.9717	0.0143	0.93
All species/age 0	1.2477	0.0448	0.77

In those cases where regression slopes differed significantly from 1, the species/age groups were generally poorly represented in trawl catches (e.g. pollock, yellowtail flounder, and winter flounder age 0). In the other cases, results indicate that the multiple regression models are relatively robust predictors of co-occurrence patterns, given annual data on species abundance and environmental preference data.

Discussion

Data developed herein on the ecological determinants of fish distributions are indicative of a complex set of interactions among the demersal fish fauna of Georges Bank and their environment. The Georges Bank area is characterized by substantial variability in bottom water temperature at depth (Fig. 2 and 3). In shallower depths (<100 m) this variability may be as much as 15° between seasons. Beyond 250 m, however, the variability in temperature decreases markedly. Some of the species/age groups exhibited distinct preferences for relatively narrow depth ranges (as exhibited by between-season CV's in mean depth at capture) and were thus subjected to a higher degree of variability in temperature at capture (e.g. Atlantic cod, yellowtail flounder, and winter flounder). Other species, such as silver and red hakes, showed substantially less variability in temperature at capture, but were found in a much more varied depth regime (Fig. 5). The propensities of the species/age groups to "prefer" particular temperature/depth conditions are probably variously related to (1) the distribution patterns of important prey (benthic feeders such as haddock and the two flounders showed greater depth preference, while silver and red hakes, consuming crustaceans and fish, exhibited a higher degree of temperature preference), (2) upper and lower tolerable temperature values for the fishes (some are at the extreme southern extent of the species range (haddock, cod, yellowtail flounder)), and (3) seasonal movements, particularly in relation to spawning and subsequent juvenile dispersal (e.g. silver hake spawn in shallow areas of Georges Bank during the summer).

These data have been analyzed assuming Georges Bank to be a homogeneous unit of uniform temperature/depth relationship. There is in fact substantial spatial variability in temperature at depth within season, since the northern rim of the Bank fronts the Gulf of Maine (a deep, cold-water basin), while the southern edge of the Bank interacts with warmer shelf/slope water influenced by the Gulf Stream. The simplifying assumption of Georges Bank as a homogeneous unit with respect to temperature at depth is an obvious source of model error in relationship between overlap in environmental preferences and predicted frequency of co-occurrence. Given the survey stratification scheme, however, it is likely that each area of the Bank received nearly proportional sample (station) allocation, and thus the bias is reasonably constant.

Another simplifying assumption of the analysis is that of between-year variability in the temperature regimes of the Bank for a given season. Species distributed primarily by depth are likely to be relatively unaffected by all but extreme temperature fluctuations. Species seeking primarily optimal temperature regimes are, however, likely to show marked differences in spatial distribution if interannual variability in temperature at depth is great. In the latter case the degree of variability in species co-occurrence, and hence the potential for unanticipated bycatch interactions, is increased. The availability of the resources to fisheries and thus the catchability (density) of the species may be significantly altered if spatial aggregation patterns change in relation to the availability of preferred temperature/depth space. Analyses of dispersion indices in relation to the availability of preferred temperature/depth conditions (percent bottom area) would be a logical approach to identifying those species/ages likely to exhibit significant changes in availability/catchability in response to temperature fluctuations.

Relationships between overlap in temperature/depth preferences (based on patterns observed in bottom trawl surveys) and species co-occurrence are significant for most species/age combinations (Table 9). Because the datum used to measure co-occurrence (presence/absence) is significantly influenced by species abundance, a further elaboration of the model incorporating the survey abundance indices for pairs of species in addition to their temperature/depth preferences improved all model fits substantially (Table 10). The resulting regression equations appear to be useful long-term predictors of species co-occurrence, as the forecast values for 5 yr of autumn survey data collected subsequent to the study time series were significantly correlated with observed data.

An important, and unexpected, result of these analyses is the lack of correlation between indices of abundance of various species/ages and corresponding spatial dispersion statistics. Thus, the degree of contagiousness in the populations did not significantly change (either increasing or decreasing), with rather extreme (in some cases) fluctuations in population abundance. This has obvious importance not only with respect to inferences regarding technological (bycatch) interactions, but in analyzing biological interactions (predator/prey and competition) among species/age groups as well. The lack of significant "dipsersal" of the stocks with increasing abundance

may indicate that (1) the species/age groups are incapable of occupying territory outside their preferred temperature/depth range, (2) preferred prey items occur in such a restricted environmental space so as to preclude switching to alternative prey in other areas, and/or (3) physical mechanisms act to concentrate juvenile and adult fish in certain local areas from which they do not disperse. Significant changes in the spatial aggregation patterns (with abundance) would potentially have important impacts on the trophic dynamics of interacting stocks. Given prey population abundance held constant, decreasing predator abundance with increasing population contagion may result in depensatory predation mortality on preferred prey (and of course vice versa). Likewise, significant changes in the spatial aggregation patterns of fishes would have important consequences for interpretation of single and multispecies harvesting data. Changing spatial aggregation patterns imply interannual variability in availability and catchability of the species/age groups to fisheries, and thus nonlinear relationships between catch per unit effort (CPUE) and population abundance.

Environmental overlap coefficients (Tables 4 and 5) and analyses of species co-occurrence are useful for identifying the potential for biological interaction (predator/prey and competition) between species/age pairs. Spatial overlap (as determined in part by temperature/depth preferences) is a requisite for such interactions. In the absence of synoptic sampling of food habits in time and space, spatial overlap coefficients may be important sources of ancillary data in modeling biological interactions.

Trawl fisheries on Georges Bank are characterized by substantial variability in species composition of landings by year, subarea, and season (Mayo et al. 1981; Murawski et al. 1983). Interannual variability in catch composition is primarily due to differential recruitment and harvest rates among exploited stocks. Differing species compositions between areas and seasons are a result of the changing aggregation patterns of various species, in relation to the prosecution of semidiscrete "fisheries," defined on the basis of effort directed to particular target species (Murawski et al. 1983). Our results present an ecological basis for the differential species compositions in landings from mixed-species fisheries. For example, the relatively close association between age 1+ cod and haddock, both in temperature/depth preferences (Fig. 4) and proportional co-occurrence, is confirmed by the species composition of landings (Murawski et al. 1983). For these species the ability to selectively harvest one but not both, based on seasonal separation of the stocks (in relation to temperature/depth preferences), is remote. Such a strategy may, however, be feasible for species exhibiting a greater degree of seasonal segregation. Age 1+ haddock and yellowtail flounder have minimal temperature/depth overlap in winter and autumn (Tables 4 and 5). Conditional co-occurrence of yellowtail flounder, given haddock catch, and vice versa (0.41 in both cases), is lowest during the autumn. Thus, by prosecuting these fisheries primarily during this season, it may be feasible to minimize technological interactions and thus more fully realize management objectives simultaneously for the two stocks. Additional analyses necessary to evaluate such a harvest strategy include estimates of the seasonal availability (spatial aggregations) to assess the feasibility of fishing operations for the species during periods of maximum spatial separation (e.g. seasonal CPUE for both species). Although it may be possible to minimize the potential for technological interactions by exploiting the spatial segregation patterns of species pairs, the fact that about 10 species contribute significantly to the landings decreases the likelihood that a single pattern of seasonal harvesting will result in "optimal" single-species exploitation rates for all species simultaneously. Quantitative optimization procedures could be useful in identifying various seasonal/spatial harvest patterns that minimize the potential for under- or overfishing various constituent resources while maximizing total multispecies harvests. Because of the correlation between the degree of species co-occurrence and abundance (Table 10), accurate bycatch projections are highly dependent on the veracity of single-species catch and recruitment forecasts for future fishing seasons. Additional research on the utility of trawl survey abundance indices of both prefishery recruits and exploitable sizes in predicting the magnitude of technological interactions (as reflected in bycatch ratios from fishery catch data) thus seems warranted.

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Behaviour and Vocalizations of Two Single Sperm Whales, *Physeter macrocephalus*, Off Nova Scotia

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Mullins, J., H. Whitehead, and L. S. Weilgart. 1988. Behaviour and vocalizations of two single sperm whales, *Physeter macrocephalus*, off Nova Scotia. Can J. Fish. Aquat. Sci. 45: 1736–1743.

During June 1986, two male sperm whales, *Physeter macrocephalus*, on the Scotian Shelf were tracked by listening for their clicks with a directional hydrophone for periods of 12.5 and 7 h, respectively. Each whale travelled along the edge of the shelf at about 2 kn (3.6 km/h), and one whale, on two occasions at least, dived to the ocean floor. After about 30 min underwater, the whales spent approximately 9 min at the surface breathing. When the whales were visible at the surface, they were silent, except on one occasion when "slow clicking" (mean interclick interval of 4.6 s) was heard from Whale 2. While underwater, most of the sound production consisted of "usual clicks" (mean interclick interval 0.96 and 0.69 s for the two whales) interrupted by frequent short silences (mean durations 21.06 and 27.82 s) and occasional "creaks" (with interclick intervals less than 0.2 s) and "slow clicks." No "codas" (stereotyped patterns of clicks) were heard from these two single whales. These results are consistent with the hypotheses that "usual clicks" and "creaks" are used for echolocation and "codas" for communication.

En juin 1986, deux cachalots macrocéphales (*Physeter macrocephalus*) mâles de la plate-forme Scotian ont été suivis au mo9yen d'un hydrophone directionnel pendant des périodes respectives de 12,5 et 7 h. Chaque cachalot s'est déplacé le long du bord de la plate-forme à une vitesse de 2 km (3,6 km/h) environ, et à deux reprises, au moins, un des cachalots a plongé au fond de l'océan. Après avoir passé environ 30 min sous l'eau, les cachalots sont remontés à la surface pendant près de 9 min pour respirer. Lorsqu'ils étaient visibles à la surface de l'eau, ils étaient silencieux, sauf à une occasion où l'on a entendu un « clic lent » (intervalle moyen entre les clics de 4,6 s) émis par le cachalot numéro 2. Lorsqu'ils étaient sous l'eau, presque tous les sons produits étaient des « clics ordinaires » (intervalle moyen entre les clics de 0,96 et 0,69 s pour les deux cachalots) interrompus par des silences courts fréquents (durée moyenne de 21,06 et 27,82 s), et des « gémissements » occasionnels (avec des intervalles entre les clics de moins de 0,2 s) et des « clics lents ». Aucun code (représentations stéréotypées de clis) provenant de ces deux cachalots n'a été entendu. Ces résultats sont conformes aux hypothèses selon lesquelles les « clics ordinaires » et les « gémissements » servent à l'écholocation et les codes à la communication.

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Until recently, most available information on the behaviour of sperm whales, *Physeter macrocephalus*, was based on observations made "at one moment in time (normally after death)" (Best 1979). However, during the past 5 yr, techniques have been developed for the study of the behaviour of living sperm whales for extended periods of time (Whitehead and Gordon 1986). These techniques are based on tracking sperm whales from sailing vessels passively using a directional hydrophone, identifying individuals using photographs of natural markings, and following them underwater with a recording depth sounder. This research has almost entirely concerned groups of sperm whales, and especially groups of females with their calves, which generally inhabit tropical waters. Important results have been obtained on the social organization of sperm whales in two principal study areas, off Sri Lanka and the Galapagos Islands (Gordon 1987; Whitehead and Arnbom 1987), but during these studies, there were no opportunities to track individual sperm whales for considerable periods. Male sperm whales, as they grow, are found at generally higher latitudes and in smaller groups (Best 1979), so better opportunities for finding and tracking single sperm whales are likely to exist away from the tropics.

Studies of single animals over extended periods of time are vital for an understanding of feeding patterns, diving behaviour, respiration, energetics, and diurnal patterns as well as the population variation of these variables. Like many other cetaceans, sperm whales are vocal, although, unusually, their vocalizations seem restricted to clicks (Backus and Schevill 1966). However, they can use clicks in a number of ways: regularly spaced clicks at various repetition rates, high repetition rate "creaks," and stereotyped patterns of clicks called "codas" (Backus and Schevill 1966; Watkins and Schevill 1977; Watkins 1980). Studies of individual animals over extended periods of time in which acoustic output is related to the dive cycle and other observable behaviour will help determine the functions of the different forms of vocalization. With good correlations between vocalizations and behaviour, we can also interpolate the behaviour of whales when we can hear but not see them, such as at night.

As sperm whaling is halted, there is increasing interest in assessment methods which do not depend on catches. Acoustic and visual censuses of sperm whales are two techniques whose development is receiving special attention (Whitehead and Gordon 1986). In order to obtain absolute estimates of abundance from such censuses, it is necessary to know the statistical properties of the time each individual spends at the surface (for

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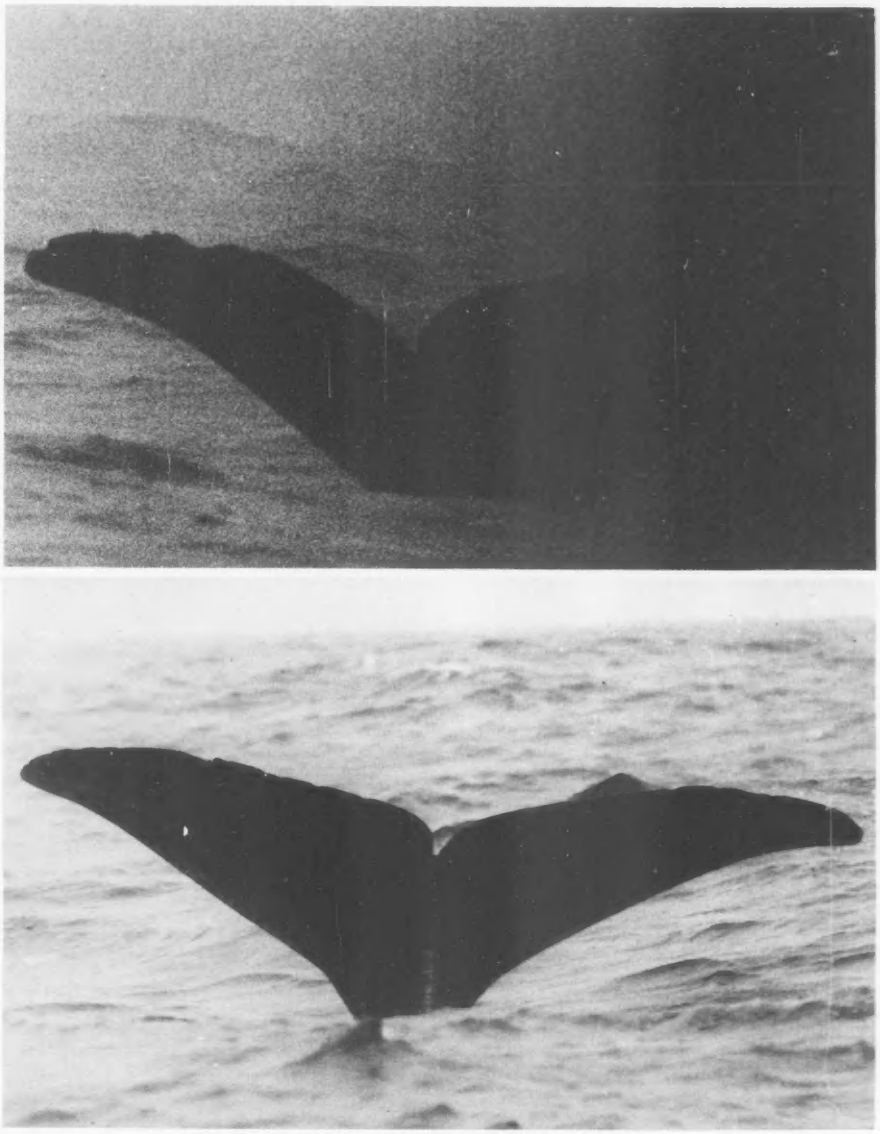

FIG. 1. Fluke photographs from Whale 1 (above) and Whale 2 (below).

visual censuses) or vocalizing (for acoustic censuses). Ideally these data should come from extended continuous studies of individual whales.

This paper reports on a study of sperm whales off Nova Scotia during the summer of 1986. Two sperm whales were tracked acoustically for periods of several hours during which their sounds were recorded continuously. The movements, diving behaviour, and acoustic output of these two whales are described and compared with results of other studies. The long continuous recordings also allow direct comparison between the acoustic output of the whale and the stage of its dive cycle.

Methods

The 10-m sloop *Elendil* with a crew of five was used to track sperm whales in an area along the continental slope off Nova Scotia (42°50′ to 43°40′N and 60°00′ to 62°50′W) from 17 to 25 June 1986.

Sperm whales were located by cruising the areas from where they have been reported (Mitchell 1975) and listening for their clicks with a Benthos AQ17 omni-directional hydrophone for 5 min every 30–60 min.

Once found, sperm whales were tracked for as long as possible by means of a Dev-Tec directional hydrophone. This hydrophone was monitored approximately every 30 min when following sperm whales to obtain bearings to, and approximate acoustic intensities of, the clicks. The course and speed of the boat, which was under sail, were adjusted to follow the track of the whales. While following whales, a continuous recording

(except for changing tapes) was made with a Benthos AQ17 hydrophone, an Ithaco 453 preamplifier (using low-frequency "roll-off" filters to minimize wave noise), and a Nagra IV SJ tape recorder (tape speeds of 1.5 and 3.75 cm/s). The recordings were continued until the whale(s) were lost or until sounds from other ships interfered with the recording.

During daylight, if the whale being tracked was visible at the surface, the number of blows, time first seen at the surface, and time of the fluke-up (flukes are shown when the whale dives) were recorded. Photographs were taken of the tail flukes with a Canon AE1 Program camera and 300-mm lens. Fluke photographs are used to identify individual animals (Arnbom 1987). A Simrad Skipper 603 recording depth sounder was used to obtain a trace of the diving whale whenever possible. Navigation was by Tracor Transtar satellite navigator. This provided positional fixes accurate to 0.2 nautical miles (0.4 km) approximately every 2 h.

The results presented in this paper are for two single whales for which the data collection was particularly clear and unambiguous: Whale 1 was recorded from 17:35 on 21 June to 07:30 on 22 June and Whale 2 from 14:20 to 21:30 on 23 June (all times Atlantic summer time, $Z + 3$). For Whale 1 the recordings of whale sounds from 05:50 to 07:30 on 22 June were obscured by noise from fishing vessels and these time periods were not included in the statistical compilation of the acoustic analysis (see Table 2; Fig. 5). There were no visual or acoustic indications of other sperm whales nearby during these periods. In other cases we were following more than one whale, or the track was of less than 2 h duration. Strong winds during the research facilitated tracking under sail but made surface observation and photography difficult. Fluke photographs (Fig. 1) showed that Whale 1 and Whale 2 were different animals. Both whales were assumed to be immature males from estimates of their length (approximately 11–13 m) and relatively large foreheads. Twenty-three percent of the sperm whales, all males, caught in the area between 1967 and 1972 were in this size range, despite selection for larger animals (Mitchell 1975).

During analysis, the acoustic recordings were broken down into the following categories: "usual clicks", "creaks", "slow clicks", short silences, and long silences. Usual clicks are series of clicks with an interval of less than 3 s between clicks but which are heard as separate distinct clicks (Weilgart and Whitehead 1988). Creaks are very rapid clicks that sound similar to a rusty door hinge. The individual clicks in a creak cannot be distinguished from one another by the human ear when the tape is played at the recorded speed (interclick interval less than 0.2 s). Slow clicks were arbitrarily designated as series of clicks having an interval of greater than 3 s between clicks (cf. Weilgart and Whitehead 1988). Short silences are less than 5 min but longer than 20 s between series of clicks. Long silences are greater than 5 min between series of clicks. "Trains" of usual clicks were separated by creaks, short silences, long silences, or slow clicks. Trains of slow clicks were separated by creaks, short silences, long silences, or usual clicks. Interclick intervals for usual clicks were measured by listening to approximately 3.5 min of randomly chosen usual clicking per tape and timing the intervals between the clicks. Interclick intervals for slow clicks were measured from all adjacent pairs of slow clicks within each train. More detailed acoustic analysis, using an oscilloscope and sound spectrograph, was hindered by loud ambient noise mainly from waves and the motion of the hydrophone through the water.

In order to estimate the average speeds of the sperm whales along the ocean floor, distances between adjacent satellite fixes were compared with the time intervals between fixes. Intervals of less than 30 min were discarded because in these cases the fixes were too close together in time to give an accurate speed.

Results

Movements of Sperm Whales

The movements of the research vessel while tracking and recording the whales provide a general description of the movements of Whales 1 and 2, since the research vessel was usually within about 2 km of the tracked whales as estimated by the strength of the acoustic contact. The whales travelled in fairly straight lines along the edge of the Scotian Shelf (Fig. 2) at about 2 kn (3.6 km/h) over the bottom (Table 1). Their tracks roughly followed bottom contours (75 m for Whale 1 and 200 m for Whale 2).

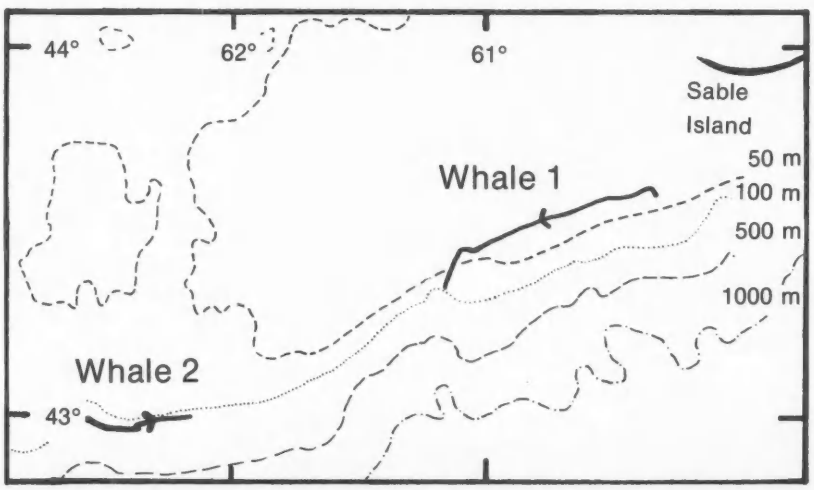

FIG. 2. Movements of the research vessel while tracking Whales 1 and 2 on the Scotian Shelf.

TABLE 1. General behaviour of Whale 1 and Whale 2.

General behaviour	Whale 1			Whale 2		
	Mean	SD	*n*	Mean	SD	*n*
Speed (km/h)	5.3	1.81	7	3.4	1.66	7
Diving descent rate (km/h)	—	—	—	5.3	—	2
Breathing rate (exhalations/min)	3.2	0.40	3	2.9	0.18	3
Observed time at surface (min)	7.7	0.33	3	9.8	1.16	3

Dive Cycle

Whale 1 and Whale 2 were each observed at the surface on three occasions (Fig. 3). These periods lasted from 6.5 to 10.5 min, with a mean of 8.7 min. All surface periods ended with a fluke-up. The recorded durations at the surface may have been underestimated, possibly by up to 2 min, because the occasion when the whale was first observed at the surface was not necessarily when it first surfaced. The breathing rates of both whales were approximately 3 exhalations/min while they were being observed at the surface (Table 1).

Two clear dive traces of Whale 2 were collected (Fig. 4). In each case, the depth sounder was turned on approximately 1 min after the fluke-up was observed. On both occasions the whale dived straight down to the bottom, at 305 and 400 m, respectively, descending at a speed of about 3 kn (5.3 km/h) (Table 1).

Intervals between observed periods at the surface were 41.7 and 31.5 min for Whale 1 and 47.5 and 52.9 min for Whale 2.

Vocalizations and the Dive Cycle

Generally, no sounds were heard from whales while they were observed at the surface (Fig. 3). Clicking stopped 0–2 min before the whale was first seen. These periods of silence were

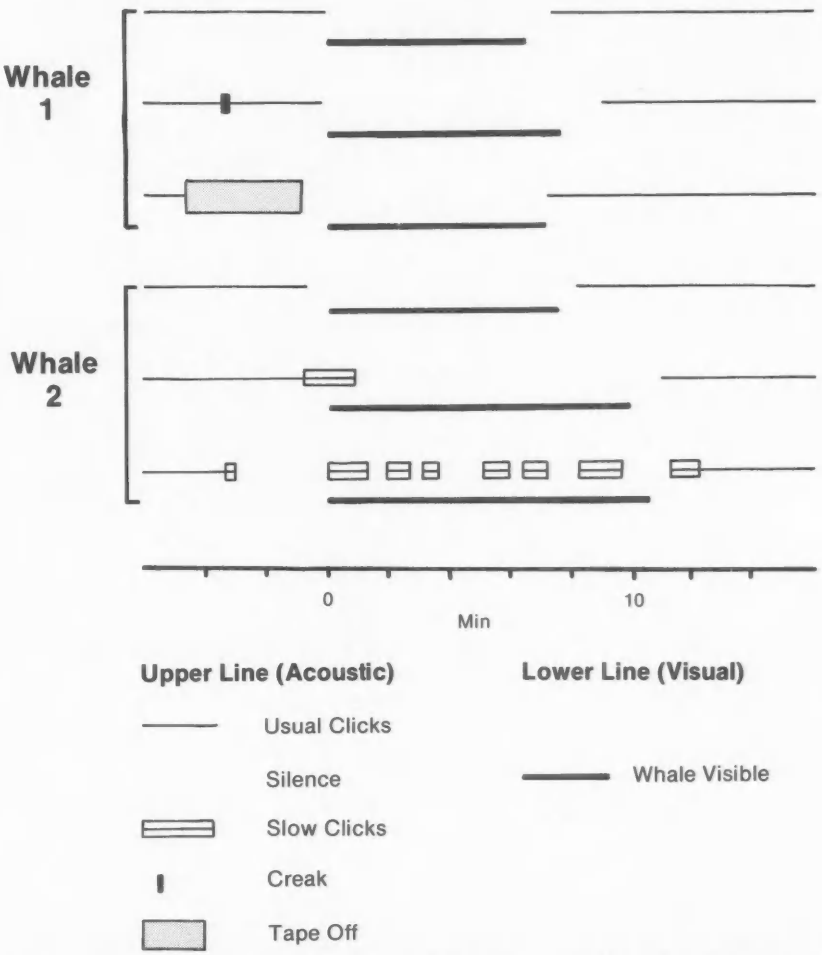

FIG. 3. Comparison between acoustic recordings and periods observed at the surface for Whales 1 and 2. In each case the upper line represents the acoustic recording and the lower the visual record of the whale at the surface. The scale on the *x*-axis is in minutes from the time at which the whale was first seen.

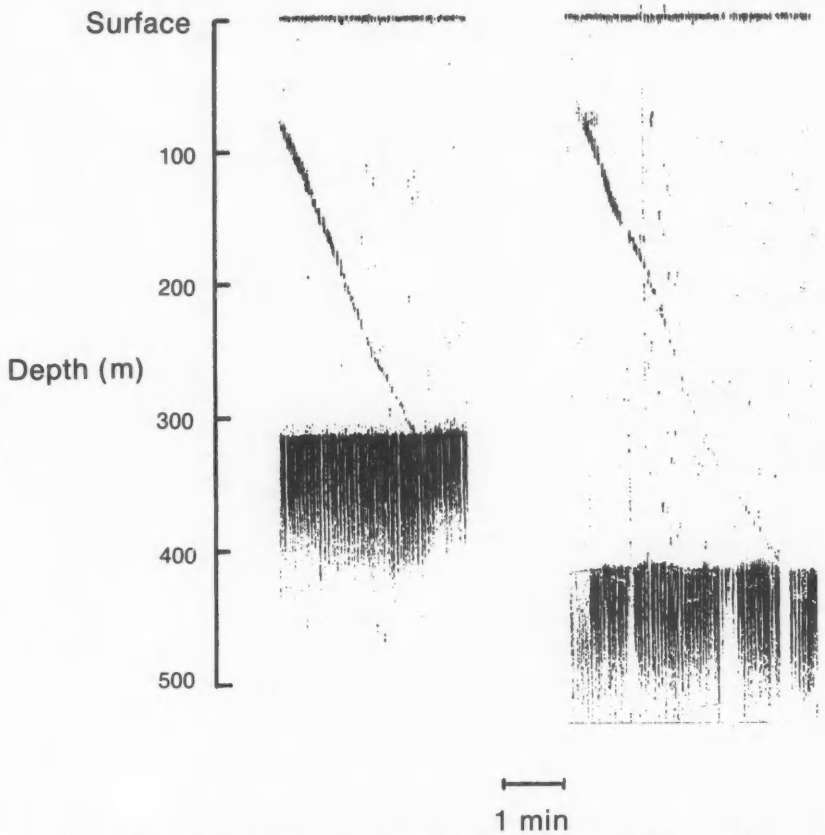

FIG. 4. Two depth sounder traces from Whale 2 (diagonal lines). The flecks on the trace are from clicks emitted by the whale.

usually preceded and followed by usual clicking. Usual clicks and creaks were never heard from a whale visible at the surface. However, on one occasion, Whale 2 produced slow clicks while it was visible at the surface and on another it made slow clicks just as it came to the surface (Fig. 3).

The median durations of the long silences and/or long slow clicking periods (of greater than 5 min), 9.0 min (Table 2), for both whales, are very similar to the mean observed times at the surface, 7.7 and 9.8 min (Table 1). Also, the intervals between observed periods at the surface (means of 36.6 min for Whale 1 and 50.2 min for Whale 2) are similar to the intervals between long silences and/or long slow clicking, medians of 27.0 min for Whale 1 and 46.5 min for Whale 2 (Table 2).

Acoustic Behaviour

The general acoustic behaviour of the two whales consisted of 30–50 min of usual clicking, alternating with 6–30 min of long silence or slow clicking (Fig. 5). The periods principally consisting of usual clicking were interrupted by short slow clicking periods, creaks, and short silences. No patterns of clicks similar to those called codas (Watkins and Schevill 1977) were heard from these single whales.

Approximately two thirds of each hour of acoustic recording consisted of usual clicking (Table 2). Usual clicking trains produced by Whale 1 were generally longer, and had a longer interclick interval, than those produced by Whale 2 (Table 2).

Both whales produced creaks. The duration of creaking trains was shorter for Whale 1 than Whale 2, but the few creaks produced by Whale 2 were highly variable in duration (Table 2). Whale 1 creaked almost twice as often as Whale 2 per hour of acoustic recording (Table 2).

Most periods of silence for Whale 1 were 15–30 s in duration whereas most silences were 7.5–15 s for Whale 2. The silences of Whale 1 were clumped into two groups, from less than 7.5 s to 2 min and from 4 to 32 min, whereas the silences of Whale 2 were distributed from less than 7.5 s to 16 min. On two occasions the whale being tracked and recorded (Whale 1) was silent for approximately 30 min (Fig. 5). It is unknown whether the whale was at the surface breathing or whether it was silent during a dive. The durations of short silences of both whales were highly variable (Table 2). Whale 2 had three times as many short silences per hour of acoustic recording as Whale 1 (Table 2).

Slow clicking was heard only from Whale 2. Slow clicking trains varied in duration (Fig. 5) and the intervals between slow clicks in a train were usually 3–8 s.

Discussion

The sperm whales tracked in this study were found and followed in locations close to the sperm whale catches off Nova Scotia between 1967 and 1972, often in water less than 200 m

TABLE 2. Summary of the acoustic behaviour of Whale 1 and Whale 2.

Acoustic behaviour	Whale 1 Mean	Whale 1 SD	Whale 1 *n*	Whale 2 Mean	Whale 2 SD	Whale 2 *n*
Usual clicks						
Train duration (min)	2.94	2.43	105	2.36	1.07	162
Interclick interval (s)	0.96	0.14	18	0.69	0.18	20
Hours usual clicking per hours acoustic recording	6.0/11.8 = 0.51			5.2/6.5 = 0.80		
Short silences						
Duration (s)	21.06	16.60	146	27.82	37.28	213
No. short silences per hour of acoustic recording	146/11.8 = 12.37			213/6.5 = 32.68		
Creaks						
Duration (s)	26.76	15.69	17	61.0	71.04	5
No. creaks per hour of acoustic recording	17/11.8 = 1.44			5/6.5 = 0.77		
Slow clicks						
Train duration (s)				32.01	23.40	41
Interclick interval (s)				4.57	1.82	40
No. slow clicking trains per hour acoustic recording	0.00			41/6.5 = 6.30		
Periods of silence or slow clicking of >5 min						
Duration (min)	9.0	7.05	17	9.0	4.77	7
Intervals between (min)	27.0	10.78	16	46.5	6.54	6

deep (Mitchell 1975). Sperm whales are generally considered deepwater animals (e.g. Caldwell et al. 1966; Berzin 1971; Gaskin 1982). However, there have been other reports in the literature of sperm whales in shallow waters. Caldwell et al. (1966) summarized accounts of sperm whales captured in depths between 73 and 162 m, as well as much deeper.

It is likely that Whales 1 and 2 swam along the edge of the Scotian Shelf in order to utilize food resources which congregate in this area. Sperm whales caught off Nova Scotia had stomach contents consisting principally of monkfish, *Lophius americanus* (V. Kozicki, Arctic Biological Station, Ste-Anne-de-Bellevue, Que. H9X 3R4, pers. comm.). The edge of the Scotian Shelf is an area where upwelling occurs (Fournier et al. 1977), and therefore, food supplies are likely to be plentiful. Gaskin (1971) noted that sperm whales may concentrate on the edges of cyclonic zones of upwelling.

The sperm whales that we tracked acoustically swam at 2 kn (3.6 km/h), similar to the 2–3 kn reported by Berzin (1971) for undisturbed animals and the 2.1 kn (SD 1.1 kn) for groups of female sperm whales with their young tracked acoustically off the Galapagos Islands (H. Whitehead, Biology Department, Dalhousie University, Halifax, N.S. B3H 4J1, unpubl. data).

The two whales followed off Nova Scotia spent almost two thirds of the time underwater. Their dive cycle consisted of about 9 min at the surface followed by a dive of about 30 min. Off the Galapagos Islands, female sperm whales were found to spend about 10 min at the surface followed by a dive of approximately 45 min (H. Whitehead, unpubl. data), although, as with the sperm whales off Nova Scotia, there was considerable variation. Other reported dive durations vary from greater than 2 h (Watkins et al. 1985) to 50 min (Clarke 1980) to less than 10 min (Lockyer 1977). In this latter case the whales were being chased by a whaling vessel and therefore probably not exhibiting normal behaviour. While at the surface the whales exhaled approximately 3 times/min which is in agreement with Gaskin (1964) who found that undisturbed sperm whales exhaled 2–3 times/min. Berzin (1971) reported a slightly higher rate of 4–6 exhalations/min. The dive rates indicated on the two recording depth sounder traces for Whale 2 of 3 kn (5.4 km/h) are almost identical to rates obtained in the same manner from diving sperm whales off Sri Lanka and the Galapagos Islands (Papastavrou 1987). The results of Lockyer (1977), who measured dive rates of sperm whales using sonar, are much more variable than those found here or presented by Papastavrou (1987). This discrepancy might be explained by difficulties in accurately estimating depths when the transducer is not vertically mounted (as was the case in Lockyer's work) and the fact that her whales were being chased by a whaling vessel. The Sri Lankan and Galapagos whales generally dove to about 410 m below the surface, although the water depth was usually greater than 2000 m (Papastavrou 1987) whereas the whales tracked off Nova Scotia seemed to dive to the shallower bottom.

Thus, some aspects of sperm whale behaviour (such as swimming speed, diving descent rate, period at the surface, and breathing rate) seem reasonably invariant of geographical area and water depth. The differences between Whale 1 and Whale 2 in dive times and some acoustic behaviour might be attributed to the different water depths in which they were swimming, different prey types, or to temporal or individual variations in behaviour. Further data, of the type presented here, would help distinguish between these possibilities.

During the dive phase of the activity cycle the whales produced clicks almost continuously. The intervals between usual clicks of sperm whales off the Scotian Shelf (means of 0.96 and 0.69 s for Whales 1 and 2) were generally in the range of those measured from whales off the Galapagos Islands (0.2–

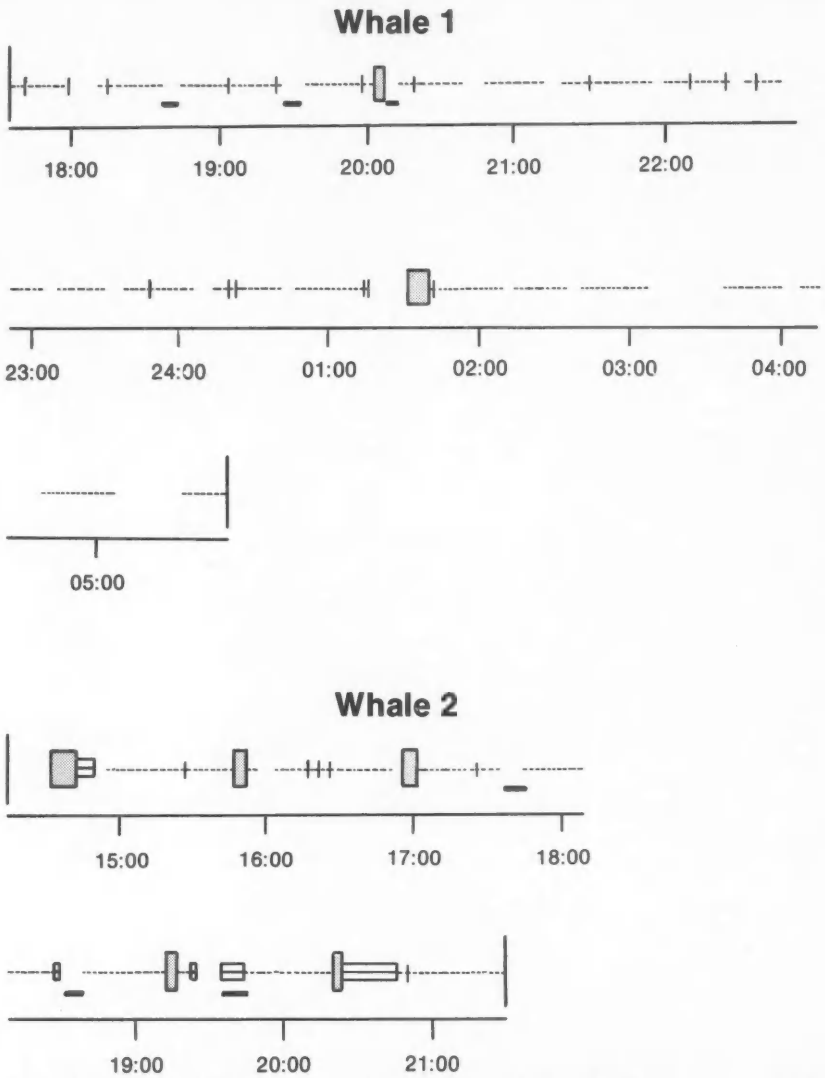

FIG. 5. Acoustic behaviour of Whales 1 and 2. In each case the upper line represents the acoustic recording and the lower the visual record of the whale at the surface. Notation is as in Fig. 3. The line representing usual clicking is broken to represent short silences. Because of the small scale of this diagram and high rate of short silences, especially for Whale 2, the correspondence between breaks in the usual clicking line and short silences is not always one-to-one. For similar reasons, some short slow clicking trains are joined.

1.0 s; Weilgart and Whitehead 1988) and the repetition rates of 0.025–1.250 clicks/s given by Backus and Schevill (1966). Backus and Schevill (1966) and Norris and Harvey (1972) hypothesized that these usual clicks are "search mode" echolocation: the whale is scanning the ocean, not examining anything in particular, but looking for things. Although Watkins (1980) found little evidence for sperm whale echolocation, Gordon (1987) has recently presented correlations between the acoustic output and fine-scale movements of sperm whales which strongly suggest that at least some vocalizations, and especially creaks, are used to echolocate.

Creaks were emitted very infrequently. Creaks are probably produced when the whale is examining an object at extremely close range. The object might be prey, the ocean floor, or other marine organisms. Norris and Harvey (1972) noted that very high repetition rates of clicks occurred when a phonating whale swam over and hit their hydrophone. They reported rates of 60–80 clicks/s lasting a minute or more.

Slow clicks, unlike other vocalizations, were produced at the surface as well as underwater. Like usual clicks and creaks, slow clicks may function in echolocation. The interclick interval of slow clicks is much longer than that of either usual clicks or creaks, suggesting that the object of interest is at a greater distance. However, it appears unlikely that slow clicks produced while breathing at the surface were used for either nav-

igation or feeding. Weilgart and Whitehead (1988) found that slow clicks seem to be characteristic of maturing or mature male sperm whales and hypothesized that this vocalization may function in informing other whales of a male's maturity and/or competitive ability on the breeding grounds. As far as we could tell, there were no other sperm whales, and almost certainly no females, near Whale 2 when he produced slow clicks. If slow clicking is important in male mating success, practicing slow clicking before reaching the breeding grounds might be functional. Alternatively, slow clicks could have multiple functions.

Although no codas were recorded while tracking Whales 1 and 2 which were always single, codas were heard at other times during our study on the Scotian Shelf when more than one sperm whale was present. These observations support Watkins and Schevill's (1977) conclusion that codas are used for communication between sperm whales.

Our observations are not necessarily representative of the complete behaviour cycle of sperm whales: we only consider single whales, and our locating and tracking techniques may bias observations towards some subsections of the population or certain behavioural patterns. Nevertheless, the potential for further insight into sperm whale behaviour from passive observation of their behaviour and vocalizations is considerable.

Acknowledgements

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Accumulation of Mercury by Plankton and Benthic Invertebrates in Riverine Lakes of Northern Manitoba (Canada): Importance of Regionally and Seasonally Varying Environmental Factors

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Jackson, T. A. 1988. Accumulation of mercury by plankton and benthic invertebrates in riverine lakes of northern Manitoba (Canada): importance of regionally and seasonally varying environmental factors. Can. J. Fish. Aquat. Sci. 45: 1744–1757.

Mercury (Hg) concentrations in plankton and benthic invertebrates from riverine lakes of northern Manitoba were generally found to be unrelated, or inversely related, to inorganic and methyl mercury levels and Hg methylation rates in their habitats but were strongly dependent on environmental factors. The relationships suggest that the uptake of Hg by these organisms was controlled largely by suspended and sedimentary Hg-binding substances such as FeOOH, MnOOH, organic matter, sulfides, and clay. The sole exception was midsummer phytoplankton, whose Hg content was a function of Hg levels in local sediments, probably because interference by suspended detritus was minimal; during the spring flood, such interference had a predominant effect. Aeration of lake water by fluvial currents probably enhances the availability of Hg to plankton by promoting decomposition of organic matter and sulfides but decreases the availability of Hg to some benthic animals by causing MnOOH precipitation. FeOOH apparently limits Hg uptake by chironomid larvae but MnOOH limits Hg uptake by oligochaetes, nematodes, and pelecypods, suggesting preferential uptake of certain forms of Hg by particular biological and mineral species. Decreases in temperature may also retard Hg uptake by benthos. Biodilution has no significant effect on Hg accumulation by benthos or plankton.

La teneur en mercure (Hg) chez les invertébrés planctoniques et benthiques de lacs situés dans le nord du Manitoba n'était pas liée en général, ou était inversement liée, à la teneur en mercure inorganique et en méthylmercure, et au taux de méthylation du Hg dans leur habitat, mais elle était fortement dépendante de facteurs environnementaux. Le rapport semble indiquer que la fixation de Hg par ces organismes était régie en grande partie par des substances sédimentaires et en suspension fixant le Hg comme le FeOOH, le MnOOH, la matière organique, les sulfures et l'argile. La seule exception était le phytoplancton du milieu de l'été dont la teneur en Hg était fonction de la teneur en Hg dans les sédiments locaux en raison sans doute du peu d'interférence que présentaient les débris en suspension; pendant la crue printanière, cette interférence avait un effet prédominant. L'aération de l'eau du lac par les courants fluviaux augmente probablement la disponibilité du Hg pour le plancton en favorisant la décomposition de la matière organique et des sulfures mais diminue la disponibilité du Hg pour certains animaux benthiques en provoquant la précipitation du MnOOH. Il semble que le FeOOH limite la fixation de Hg par les larves de chironomidés mais le MnOOH limite la fixation de Hg par les oligochètes, les nématodes et les pélécypodes, ce qui semble indiquer une fixation préférentielle de certaines formes de Hg par des espèces biologiques et minérales particulières. Des baisses de température peuvent aussi retarder la fixation du Hg par le benthos. La biodilution n'a aucun effet important sur l'accumulation de Hg par le benthos ou le plancton.

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A previous paper (Jackson 1988b) treated the biogeochemistry of mercury (Hg), especially the production of methyl mercury (CH_3Hg^+), in sediments and water of lakes along the Churchill River diversion route in northern Manitoba, with emphasis on effects of environmental alteration caused by recent hydroelectric development. In the present paper, the accumulation of Hg by plankton and benthic invertebrates in these lakes is examined. The purpose of the study was to investigate effects of environmental factors in general, and the impact of reservoir creation in particular, on Hg levels in planktonic and benthic organisms.

Hg concentrations in the plankton and benthos of lakes in northern Manitoba have also been studied by Bodaly et al. (1987) and W. F. Warwick (National Hydrology Research Institute, 11 Innovation Blvd., Saskatoon, Sask. S7N 3H5, unpubl. data).

Field Area, Materials, and Methods

A full description of the field area, together with a detailed treatment of the collection and analysis of sediment and water samples, has been given elsewhere (Jackson 1988b). Briefly, the samples for the present study were taken from Granville Lake, Southern Indian Lake, (South Bay and a shallow cove of Long Bay (= Wupaw Bay)), and selected lakes of the "Notigi

Reservoir'' complex (Rat Lake, Central Mynarski Lake, and the east and west basins of Notigi Lake) (Jackson 1988b, fig. 1).

Granville Lake (the ''control'' region) has not been altered by the Churchill River diversion, while the other lakes have been affected to different degrees by the impoundment and rerouting of river water and resultant flooding of adjacent land. The impact of flooding on the aquatic environments, including the subsequent increase in rates of CH_3Hg^+ production in sediments and CH_3Hg^+ accumulation by fish, has tended to increase in the order Granville Lake < Southern Indian Lake < Notigi Reservoir lakes (Bodaly et al. 1984; McGregor 1980; Jackson 1988b). Superimposed on these general effects of recent flooding are the following geographical variations in the lacustrine environments (Jackson 1988b): (1) ''main-stream'' regions are vigorously flushed by river water flowing through them, while ''backwater'' regions are quieter and less rapidly flushed; therefore, backwater environments are influenced to a greater extent by local drainage and accumulate higher concentrations of allochthonous organic matter derived from local forest soils and muskeg (Jackson and Hecky 1980); (2) South Bay is bordered by Pleistocene silty clay deposits which are undergoing erosion, causing locally elevated turbidity that decreases gradationally in the order South Bay > Rat Lake > Notigi Lake; (3) Granville Lake and the west basin of Notigi Lake have certain anomalies in common, such as high primary productivity (Bodaly et al. 1987; Jackson 1988b), the presence of manganese nodules, and sediments with elevated manganese/iron (Mn/Fe) ratios and low clay concentrations, which set them apart from the other regions and suggest exceptionally vigorous mixing, agitation, and aeration (Jackson 1988b).

Samples of >10 μm plankton were taken during 23–25 June (the time of the spring flood) and 11–13 August 1981. Integrated water samples were collected with a flexible plastic tube lowered to about twice the depth of visibility as determined with a Secchi disk, and the plankton was filtered out by passing known volumes of this water through a 10-μm net designed to trap phytoplankton (except for the tiny ''picoplankton species (Stockner and Antia 1986)) together with zooplankton. The plankton samples were freeze-dried and stored for chemical analysis.

Benthic macroinvertebrates (see also W. F. Warwick, unpubl. data) were sampled during 23–25 June 1981. Bottom sediments were collected with an Ekman dredge 15.2 × 15.2 cm in cross section, and the fauna was isolated by screening the sediment through a 200-μm net. The different taxonomic types were then separated, identified, weighed, frozen at −40°C, and stored for chemical analysis. Before being frozen, chironomid larvae were bathed in water, with daily changes of water, for 2–3 d without food to void their gut contents. This procedure was not feasible with the other types of invertebrates.

All biological specimens were wet-ashed and analyzed for total Hg by flameless atomic absorption spectrophotometry (Jackson 1988b). The plankton samples were digested with H_2SO_4, HNO_3, and $KMnO_4$ (Armstrong and the Uthe 1971), and the benthic invertebrates were digested with H_2SO_4, HNO_3, HCl, $KMnO_4$, and $K_2S_2O_8$ (Mercury Sampling and Analysis Review Committee 1977). Hg data for benthic invertebrates were computed on the basis of fresh weight and data for plankton on the basis of dry weight. Replicate analyses were performed on three of the benthic invertebrate (chironomid) samples. Owing to the small sample sizes, however, only single analyses could be performed on the other samples.

Samples of zooplankton were not available for analysis, but Hg data for >73 μm zooplankton collected from the same sampling areas by other workers were obtained from the literature (Bodaly et al. 1987). The zooplankton samples were collected with horizontally towed nets during 18–20 June and 17–19 August 1981 and were stored in the frozen state before being analyzed for Hg. The data were computed on the basis of dry weight.

The Hg data for the planktonic and benthic organisms were correlated with various analytical data representing sediments and water collected from the same sampling sites in 1981 and 1983. The data for the sediment and water samples, an account of the methods used for collecting and analyzing these samples, and definitions of the biogeochemical parameters employed have been published elsewhere (Jackson 1988b). The following definitions are explained in full in Jackson (1988b) but are briefly repeated here for the reader's convenience: (1) the ''available inorganic Hg'' fraction of bottom sediment = all Hg extracted with N_2-purged 0.5 M $CaCl_2$; (2) the sediment's ''total organic Hg'' fraction = Hg extracted by the procedure used for extracting CH_3Hg^+ and subsequently determined as total Hg rather than CH_3Hg^+ as such; and (3) the sediment's ''Hg methylating capability'' (or relative rate of methylation) = the quantity of CH_3Hg^+ generated by 10 g of sediment dispersed in 20 mL of 10 μM $HgCl_2$ solution when incubated for 10 d at 25°C under an atmosphere of N_2.

Relationships between data were assessed by regression analysis. Correlation coefficients (r) and significance probabilities (P) were computed for linear, log–log, semi-log, parabolic, and hyperbolic regression lines, and the regression formulas yielding the highest r and P values were selected as the nearest approximations of the trends. A relationship was defined as ''significant'' if $P \leq 0.05$.

Results and Discussion

Hg levels in plankton and benthic invertebrates varied systematically as functions of certain environmental parameters; but, except in the case of >10 μm plankton sampled in August, they showed no significant relationship — or, surprisingly, showed an inverse relationship — with the total Hg, particulate Hg, and CH_3Hg^+ content of the water and the total Hg, CH_3Hg^+, and available inorganic Hg content and Hg methylating capability of the bottom sediment. Thus, with the exception of >10 μm plankton in August, Hg concentrations in plankton and benthos were entirely, or almost entirely, independent of the environmental effects of hydroelectric development. This is remarkable, because flooding due to hydroelectric development has caused a pronounced increase in the Hg methylation rates and concentrations of CH_3Hg^+ and total Hg in sediments (Jackson 1987, 1988b; Ramsey and Ramlal 1987) and the Hg content of fish species such as walleye (*Stizostedion vitreum*) and northern pike (*Esox lucius*) (McGregor 1980; Bodaly et al. 1984).

Hg in Plankton

Plankton sampled in June

The Hg content of >10 μm plankton collected in June was highest in the rapidly flushed, well-aerated mainstream regions and lowest in the relatively stagnant backwater regions and appeared to be entirely unaffected by postimpoundment flooding due to hydroelectric development (Table 1). The plankton

TABLE 1. Hg content of >10 μm and >73 μm plankton collected in June and August 1981. The data for >73 μm plankton were taken from Bodaly et al. (1987) and recalculated. n.d. = no data.

	Hg concentration (nmol/g dry wt.)			
	June		August	
Sampling site	>10 μm	>73 μm	>10 μm	>73 μm
Granville Lake	5.48	0.10	3.2	6.13
East Mynarski Lake	n.d.	0.19	n.d.	1.9
Southern Indian Lake				
Long Bay (shallow cove)	5.33	n.d.	6.28	n.d.
Long Bay (main basin)	n.d.	0.17	n.d.	n.d.
South Bay	10.5	0.50	3.1	0.1
Notigi Reservoir				
Rat Lake	n.d.	n.d.	1.6	n.d.
West Mynarski Lake	n.d.	0.55	n.d.	1.4
Central Mynarski Lake	4.2	0.25	n.d.	0.2
Notigi Lake (west basin)	6.43	0.50	10.3	4.2
Notigi Lake (east basin)	n.d.	0.28	7.03	4.4

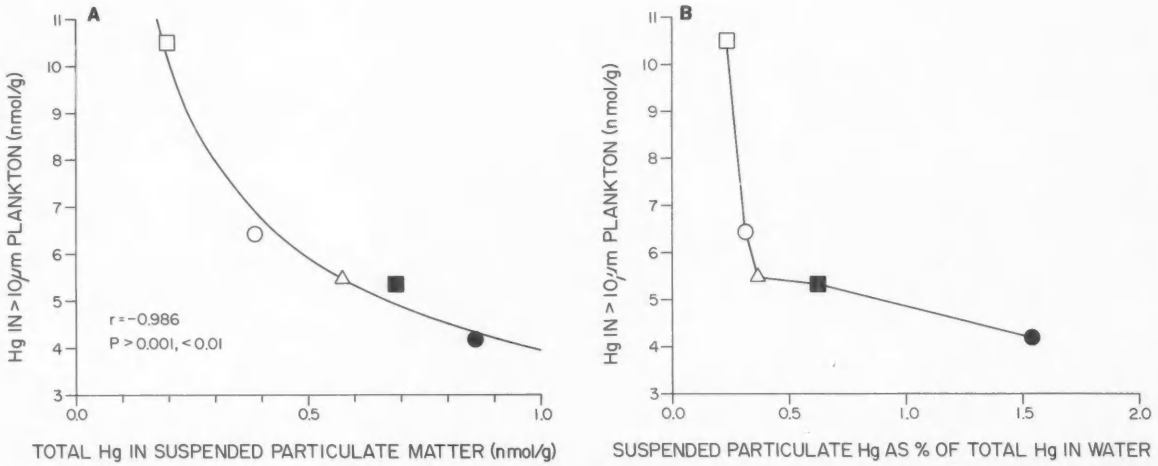
A
B
Hg IN >10μm PLANKTON (nmol/g)
r = −0.986
P > 0.001, < 0.01
TOTAL Hg IN SUSPENDED PARTICULATE MATTER (nmol/g)
SUSPENDED PARTICULATE Hg AS % OF TOTAL Hg IN WATER

FIG. 1. Relationship between Hg in >10 μm plankton collected in June 1981 and the total suspended Hg expressed as (A) concentration per unit weight of suspended matter and (B) percentage of the total Hg in the water. Solid symbols, backwater sites; open symbols, mainstream sites. △, Granville Lake; □ or ■, Southern Indian Lake; ○ or ●, Notigi Reservoir lakes.

from South Bay in Southern Indian Lake was richest in Hg, the plankton from Central Mynarski Lake in Notigi Reservoir was poorest in Hg, and plankton from other Southern Indian Lake and Notigi Reservoir sites and from Granville Lake was intermediate (Table 1). This was unexpected because the results of previous research on the effects of reservoir creation on the bioavailability and bioaccumulation of Hg in lakes of northern Manitoba (Jackson 1987, 1988b; Bodaly et al. 1984) suggest that the Hg content of the plankton ought to increase in the order Granville Lake < Southern Indian Lake < Notigi Reservoir lakes. Nevertheless, these findings were corroborated by the Hg data for the >73 μm plankton (Table 1). Thus, >10 μm and >73 gm plankton samples collected and analyzed independently by different workers indicated comparable geographic patterns of variation. However, the distinction between mainstream and backwater samples was less clear-cut in the >73 μm plankton (Table 1). The >73 μm plankton samples with the lowest Hg content came from the "control" site on Granville Lake, which has a mainstream environment.

Unexpectedly, the concentration of Hg in >10 μm plankton gave a significant *negative* correlation with the concentration of Hg in the suspended particulate matter in the ambient water (Fig. 1A). Essentially the same result was obtained if the abundance of particulate Hg was expressed as percentage of the total Hg burden of the water (Fig. 1B) or as quantity of particulate Hg per unit volume of water ($r = -0.883$; $0.05 > P > 0.02$). Similarly, the Hg content of the plankton was inversely related to the sulfide content of the bottom sediment (Fig. 2). Hg levels in the >10 μm plankton also gave statistically insignificant negative correlations with CH_3Hg^+ levels in bottom sediment and water, with total Hg and $CaCl_2$-extractable Hg concentrations in sediments, and with the sediment's relative rate of CH_3Hg^+ production as represented by its "Hg methylating capability" and gave an almost totally insignificant positive correlation with the total Hg content of the water (Table 2).

A striking feature of the curves in Fig. 1A, 1B, and 2 is the distinct separation of data for mainstream and backwater sites. Another noteworthy observation is that the curves in Fig. 1B and 2 are essentially hyperbolic.

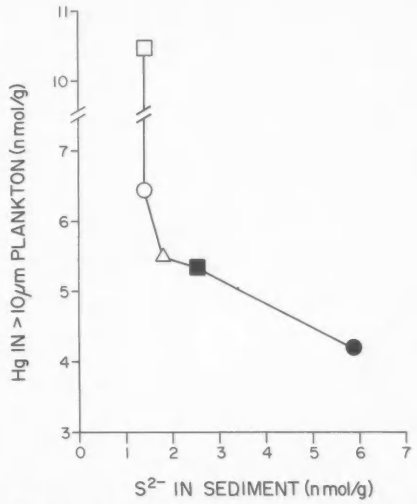

FIG. 2. Relationship between the Hg content of >10 μm plankton collected in June 1981 and the nonvolatile sulfide (S^{2-}) content of the bottom sediment. Explanation of symbols same as in Fig. 1.

In addition, the Hg content of >10 μm plankton decreased logarithmically with increasing concentration of organic matter in the sediment (Fig. 3A). A plot of Hg in >73 μm plankton against the organic carbon (C) content of the sediment gave similar results (Fig. 3B), except that the plot is split into two separate curves differing greatly in slope and diverging widely, although both are logarithmic; samples from the Notigi Reservoir lakes, which have been more extensively altered by post-impoundment flooding and whose sediments are richer in organic C, show a much more gradual decline in the Hg content of >73 μm plankton than do samples from Southern Indian Lake and Granville Lake, which were altered to a considerably lesser extent or (in the case of Granville Lake) not at all, and whose sediments have lower concentrations of organic C.

Hg levels in >10 μm plankton showed a weak inverse relationship with the concentrations of organic C ($r = -0.849$; $0.1 > P > 0.05$) and total nitrogen (N) ($r = -0.825$; $0.1 > P > 0.05$) in the bottom sediments but gave a very significant *positive* correlation with the organic C/N ratio of the sediment (Fig. 4A). Hg levels in >73 μm plankton gave similar results (Fig. 4B) except that in South Bay, which has an anomalously heavy load of suspended clay and silt, the Hg content of the plankton is much lower than the value predicted by the regression formula for the other data, causing the curve to level off abruptly.

The results presented in Tables 1 and 2 and Fig. 1–4 suggest that Hg uptake by >10 μm and >73 μm plankton sampled in June was regulated principally by the bioavailability of Hg in the environment, not by the total abundance of either inorganic (nonmethyl) Hg or CH_3Hg^+. According to this interpretation, the availability of Hg to plankton decreased with increasing concentrations of suspended and sedimentary organic matter and sulfides owing to the tendency of these substances to bind Hg strongly. Both organic C and sulfide are most abundant in poorly flushed backwater environments because organic matter derived from the surrounding heavily forested and muskeg-covered land accumulates there (Jackson 1988b). They are least abundant in mainstream environments, presumably because of rapid flushing and dilution, as well as accelerated decomposition by oxidation. Consequently, in backwater regions the amount of Hg fixed in biologically unavailable forms by nonliving particulate matter is probably higher in proportion to the amount of Hg taken up by plankton than is the case in mainstream regions. We may tentatively conclude that the observed geographical variations in the Hg content of the plankton were determined primarily by the environmentally dependent variations in the outcome of this partitioning process.

This interpretation is supported by the following facts: (1) mainstream bottom sediments had the greatest abundance of $CaCl_2$-extractable Hg per unit amount of total Hg, indicating the highest degree of Hg availability, even though Hg in plankton did not correlate with $CaCl_2$-extractable Hg; and (2) the $NH_2OH{\cdot}HCl$-extractable oxides of mainstream sediments had the highest Mn/Fe ratios, suggesting that the most highly oxidizing conditions occurred in the mainstream zone (Jackson 1987, 1988b). The positive correlation between the Hg content of >10 μm and >73 μm plankton and the organic C/N ratio of bottom sediment is another reflection of this phenomenon. The more intense the decomposition of organic matter, the higher the C/N ratio of the residue because of preferential decomposition of labile nitrogenous organic compounds (Kemp 1971). Consequently, the organic C/N ratio of the sediment as well as the Hg content of plankton tends to be highest in the vigorously agitated, well-aerated mainstream environments. The anomalous results obtained for South Bay (Fig. 4B) may well signify that the exceptionally large quantity of suspended clay and silt at that site suppresses the uptake of Hg by zooplankton or gives rise to an aberrantly high organic C/N ratio in the sediment, owing, perhaps, to some process such as preferential adsorption of the more C-rich, higher molecular weight humic fractions by the clay. Site-dependent differences in the species composition of the plankton communities could conceivably have played a role as well, but the information required to assess this possibility is lacking.

Theoretically, high C/N ratios could also represent high ratios of allochthonous (terrestrial) to autochthonous (aquatic) organic matter (Hutchinson 1957; Jackson 1988b), but this is unlikely in the present case. If this were the correct explanation, backwater regions and the environments most strongly affected by flooding would have given the highest C/N ratios.

Variations in the total biomass of the aquatic community leading to different degrees of "biodilution" of the available Hg (Jernelöv et al. 1975) can be ruled out as an important factor in explaining the variations in the Hg content of the plankton, as there is no evidence of a significant connection between Hg concentration (Table 1) and biological productivity (Jackson 1988b, table 8). There is indeed a negative correlation between Hg levels in >10 μm plankton and the mean primary productivity of the sampling region for the period 18 June to 17 August 1981, but it is very insignificant ($r = -0.642$; $P >> 0.1$). Hg in >73 μm plankton gave comparable but even more insignificant results ($r = -0.312$; $P >> 0.1$).

The observation that the Hg data for >73 μm plankton, in contrast with >10 μm plankton, form two separate and divergent curves when plotted against the organic content of the sediment — one for Southern Indian Lake and Granville Lake combined and another one characterized by a lower slope and higher Hg levels per unit concentration of organic matter for Notigi Reservoir lakes (Fig. 3) — has interesting implications from the standpoint of food-chain effects. The fact that Hg data for >73 μm plankton from main-stream and backwater environ-

TABLE 2. Correlation matrix relating the Hg content of >10 μm and >73 μm plankton to the Hg chemistry of the associated water and sediment. — = data not computed because not relevant.

	Hg in plankton							
	June				August			
	>10 μm		>73 μm		>10 μm		>73 μm	
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Total Hg in June 1981 sediment	−0.573	>>0.1	−0.427	>>0.1	−0.457	>>0.1	−0.482	>>0.1
Total Hg in Aug. 1981 sediment	−0.748	>>0.1	−0.995	>0.001, <0.01	−0.380	>>0.1	−0.205	>>0.1
Total Hg in Aug. 1983 sediment	−0.558	>>0.1	0.332	>>0.1	0.966	>0.001, <0.01	−0.449	>>0.1
CH_3Hg^+ in June 1981 sediment	−0.407	>>0.1	0.280	>>0.1	0.786	>0.05, <0.1	0.791	>0.1
CH_3Hg^+ in Aug. 1983 sediment	−0.217	>>0.1	0.332	>>0.1	0.945	>0.001, <0.01	0.517	>0.1
Total organic Hg in Aug. 1981 sediment[a]	—	—	—	—	0.912	>0.02, <0.05	0.956	>0.02, <0.05
Hg methylating capability of Aug. 1983 sediment[a]	−0.561	>>0.1	0.245	>>0.1	0.929	>0.001, <0.01	−0.399	>>0.1
$CaCl_2$-extractable Hg in June 1981 sediment[a]	−0.782	>0.1	0.135	>>0.1	—	—	—	—
$CaCl_2$-extractable Hg in Aug. 1981 sediment[a]	—	—	—	—	0.337	>>0.1	0.830	>0.1
$CaCl_2$-extractable Hg (Aug. 1981) × Hg methylating capability (Aug. 1983)[a]	—	—	—	—	0.900	>0.02, <0.05	0.745	>>0.1
Total Hg in June 1981 water	0.0642	>>0.1	−0.440	>>0.1	—	—	—	—
CH_3Hg^+ in June 1981 water	−0.340	>>0.1	0.179	>>0.1	—	—	—	—
CH_3Hg^+ in Aug. 1981 water	—	—	—	—	−0.589	>>0.1	0.714	>0.1
Total Hg in June 1981 suspended matter	−0.986	>0.001, <0.01	−0.707	>0.1	—	—	—	—
Total Hg in Aug. 1981 suspended matter	—	—	—	—	0.807	>0.05, <0.1	0.460	>>0.1
Suspended Hg in June 1981 water	−0.883	>0.02, <0.05	−0.509	>>0.1	—	—	—	—
Suspended Hg in Aug. 1981 water	—	—	—	—	0.392	>>0.1	−0.288	>>0.1

[a]See Jackson (1988b).

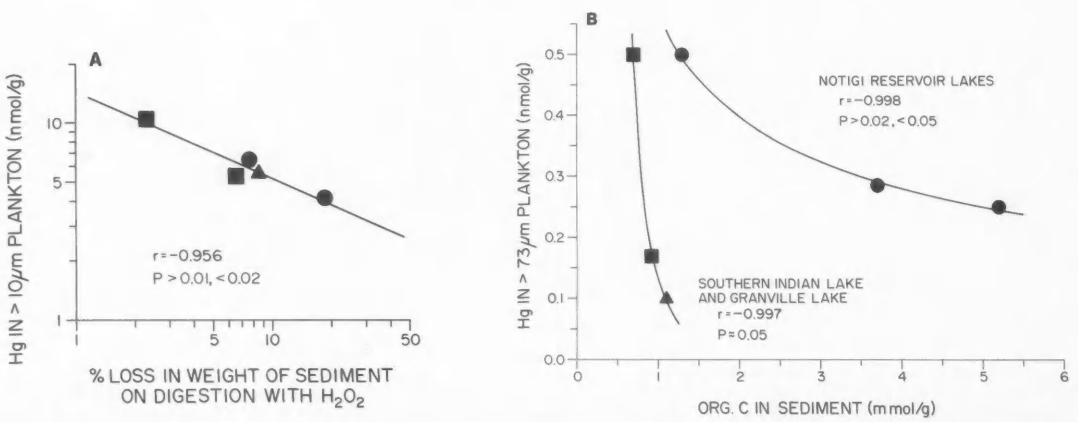

FIG. 3. Relationships between Hg in plankton collected in June 1981 and organic matter in associated bottom sediments. (A) Hg in >10 μm plankton plotted against the sediment's percent loss in weight on digestion with H_2O_2 and (B) Hg in >73 μm plankton plotted against the organic C content of the sediment. ▲, Granville Lake; ■, Southern Indian Lake; ●, Notigi Reservoir lakes.

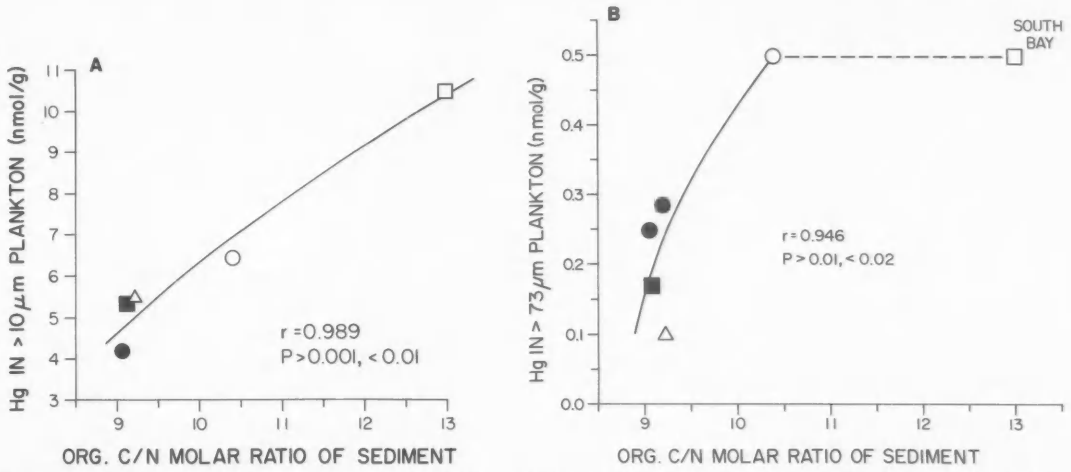

FIG. 4. Relationships between the Hg concentrations in (A) >10 μm plankton and (B) >73 μm plankton collected in June 1981 and the organic C/N ratio of the associated sediment. In Fig. 4B the regression curve represents all sampling sites except South Bay; the broken line signifies the levelling off of the curve. Explanation of symbols same as in Fig. 1. Data for >73 μm plankton from Bodaly et al. (1987).

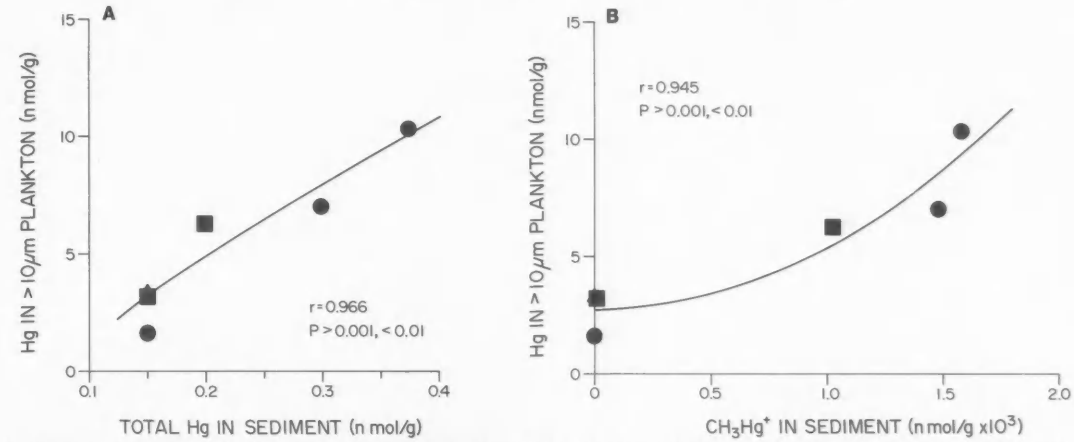

FIG. 5. Relationships between the Hg content of >10 μm plankton collected in August 1981 and the (A) total Hg and (B) CH_3Hg^+ content of bottom sediments sampled in August 1983. Explanation of symbols same as in Fig. 3.

ments are less sharply differentiated from each other than is the case with >10 μm plankton (Table 1) is also significant in this regard.

Comparison of the results obtained for >10 μm plankton (Fig. 1, 2, 3A, 4A), >73 μm plankton (Fig. 3B, 4B), and fish (McGregor 1980; Bodaly et al. 1984, 1987; Jackson 1987) provides indirect evidence that the proportion of CH_3Hg^+ to nonmethyl Hg in the aquatic organisms of northern Manitoba increases progressively up the food chain, as in other freshwater ecosystems mentioned in the literature (D'Itri 1972; Huckabee et al. 1979). At the lower end of the food chain is the phytoplankton, the dominant element of the >10 μm plankton, whose Hg content is entirely unrelated to the distribution of CH_3Hg^+ or the rate of CH_3Hg^+ production in the environment, and is therefore unrelated to effects of impoundment, but apparently depends on the bioavailability of Hg as determined by Hg-binding substances and environmental factors such as current action and aeration. At the opposite extreme, at the upper end of the food chain, are piscivorous fish such as walleye and northern pike, whose Hg levels are mainly determined by the abundance of CH_3Hg^+ and rate of CH_3Hg^+ production in the environment and therefore increase with increasing extent of postimpoundment flooding (in the order Granville Lake < Southern Indian Lake < Notigi Reservoir lakes) (Bodaly et al. 1984; Jackson 1987, 1988b) but are independent of the factors that regulate Hg uptake by phytoplankton. Zooplankton (>73 μm plankton) occupies an intermediate position in the food chain and is consequently intermediate with respect to the factors influencing the bioaccumulation of Hg (Fig. 3B). Food chain effects and accumulation of Hg by fish will be more fully treated elsewhere (T. A. Jackson, in preparation).

To summarize, the analytical data are consistent with the following conclusions: (1) the forms of Hg assimilated by the plankton are mostly inorganic (nonmethyl); (2) the availability of this Hg to the plankton is depressed when the Hg is bound by particulate organic matter and sulfides and is enhanced when

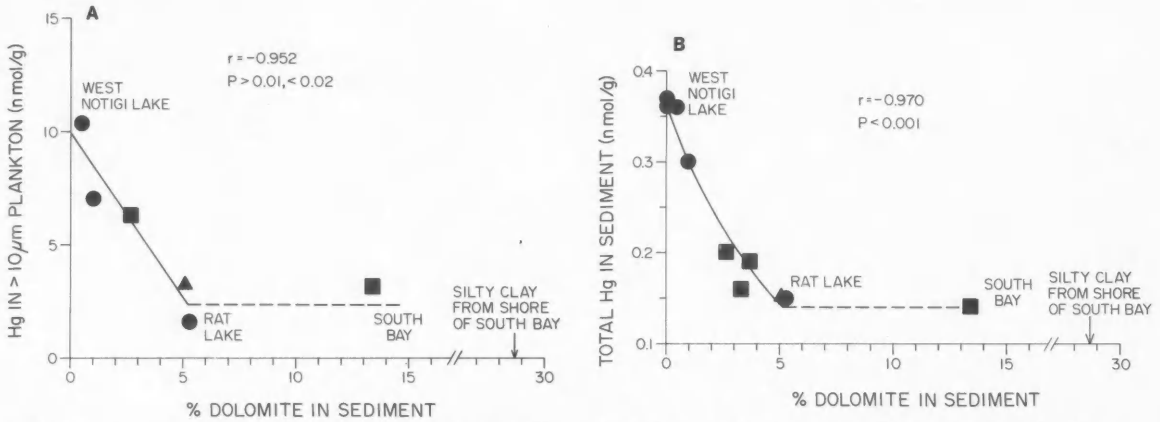

FIG. 6. Hg content of (A) >10 μm plankton collected in August 1981 and (B) sediment collected in August 1983 plotted against the abundance of dolomite in the sediment. Regression lines represent all sampling sites except South Bay; the broken lines signify levelling off of the curves. Explanation of symbols same as in Fig. 3.

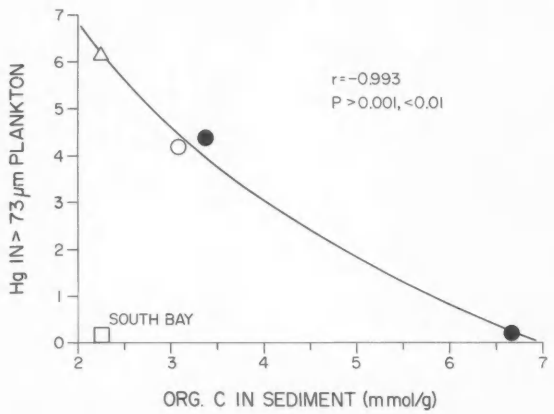

FIG. 7. Relationship between the Hg content of >73 μm plankton collected in August 1981 and the organic C content of bottom sediment sampled in August 1983. Regression curve represents all sampling sites except South Bay. Explanation of symbols same as in Fig. 1.

the Hg-binding substances are decomposed; (3) Hg availability is therefore greatest in mainstream regions, where vigorous flushing and aeration promote rapid decomposition of Hg-binding substances and release of the bound Hg; and (4) the proportion of CH_3Hg^+ to inorganic Hg is greater in >73 μm plankton than in >10 μm plankton owing to accumulation of CH_3Hg^+ up the food chain.

Plankton sampled in August

The Hg content of >10 μm plankton collected in August showed a radically different pattern of variation than the Hg content of plankton collected in June (Table 1). Hg concentrations in August plankton gave strong positive correlations ($0.01 > P > 0.001$) with the "total" (HNO_3/HCl-extractable) Hg and CH_3Hg^+ concentrations of sediments collected in August 1983 (Fig. 5A, 5B; Table 2) and with the sediment's Hg methylating capability (Table 2), and a weaker but nonetheless significant positive correlation ($0.05 > P > 0.02$) with the "total organic Hg" content of sediment collected in August 1981 (Table 2). Thus, in August, in contrast with June, the accumulation of Hg by >10 μm plankton appeared to depend simply on the total supply of inorganic Hg or CH_3Hg^+ in the environment. Again, biomass dilution seems not to have been a factor: Hg levels in the plankton gave a significant positive correlation with primary productivity measured over the interval 18 June to 17 August 1981 ($r = 0.989$; $N = 4$; $0.02 > P > 0.01$) whereas biomass dilution would have produced an inverse relationship.

Hg levels in August samples of >10 μm plankton did not correlate significantly with total Hg or CH_3Hg^+ concentrations in sediments collected in 1981 (Table 2), even though they correlated strongly with the total Hg and CH_3Hg^+ content of sediment samples collected in 1983. This probably indicates that the 1983 sediment samples happened to be more representative of those areas of the sediment–water interface which had the greatest influence on the transfer of Hg from sediments to plankton after the onset of summer stratification. At four of the six sampling regions for which August plankton data are available, the sediments were collected at shallower sites in 1983 than in 1981, and at only one site was the water deeper (Jackson 1988b, table 1). This suggests that in the midsummer, when the lakes were more or less stratified, the immediate source of the Hg taken up by phytoplankton was relatively shallow, yet fine-grained, bottom sediment in contact with the epilimnion (the habitat of the phytoplankton); the deeper sediments in the hypolimnion were probably isolated owing to stratification of the water column.

Hg levels in the >10 μm August plankton generally tended to increase with the extent of postimpoundment flooding; thus, they were highest in Notigi Lake and were relatively low in Southern Indian Lake and Granville Lake (the "control" lake). Rat Lake, however, was anomalous: although the second greatest postimpoundment rise in lake level occurred in Rat Lake, the Rat Lake plankton had the lowest Hg concentration, and the values for Rat Lake, South Bay, and Granville Lake all clustered close together at the lower end of the observed range of Hg levels. Moreover, Hg concentrations in plankton were lower in South Bay than in Long Bay, even though the rise in lake level was the same in both.

These observations appear to reflect a general tendency of flooding to release bioavailable Hg into the water, the tendency

TABLE 3. Hg content of benthic chironomids, oligochaetes, nematodes, and pelecypods collected in June 1981. Except where otherwise noted, all chironomids were larvae. $\bar{X}$ = mean; N = no. of replicate samples; n.d. = no data.

Sampling site	Hg concentration (nmol/g fresh wt.)			
	Chironomids	Oligochaetes	Nematodes	Pelecypods
Southern Indian Lake				
Long Bay (shallow cove)	1.04	3.48	2.29	1.53
South Bay	0.578	n.d.	0.546	0.115
Notigi Reservoir				
Rat Lake	0.107[a]	0.213	0.482	0.391
Central Mynarski Lake	0.0987[b]	1.68	0.816	0.0770
Notigi Lake (east basin)	0.118	0.255	0.160	0.402
	0.129[c]			

[a]$\bar{X}$ = 0.107; range = 0.0897–0.141; N = 4.
[b]$\bar{X}$ = 0.0987; range = 0.0718–0.124; N = 3.
[c]Hg content of pupae.

TABLE 4. Correlation matrix relating the Hg content of benthic invertebrates to the Hg chemistry of the associated sediment.

	Hg in benthic organisms							
	Chironomids		Oligochaetes		Nematodes		Pelecypods	
	r	P	r	P	r	P	r	P
CH_3Hg^+ in June 1981 sediment	−0.780	>0.1	−0.785	>0.1	−0.794	>0.1	−0.388	>>0.1
Total Hg in June 1981 sediment	−0.629	>>0.1	0.301	>>0.1	−0.136	>>0.1	−0.355	>>0.1
$CaCl_2$-extractable Hg in June 1981 sediment[a]	−0.789	>0.1	−0.565	>>0.1	−0.299	>>0.1	−0.347	>>0.1
Hg methylating capability of Aug. 1983 sediment[a]	−0.287	>>0.1	0.876	>0.1	0.462	>>0.1	0.374	>>0.1

[a]See Jackson (1988b).

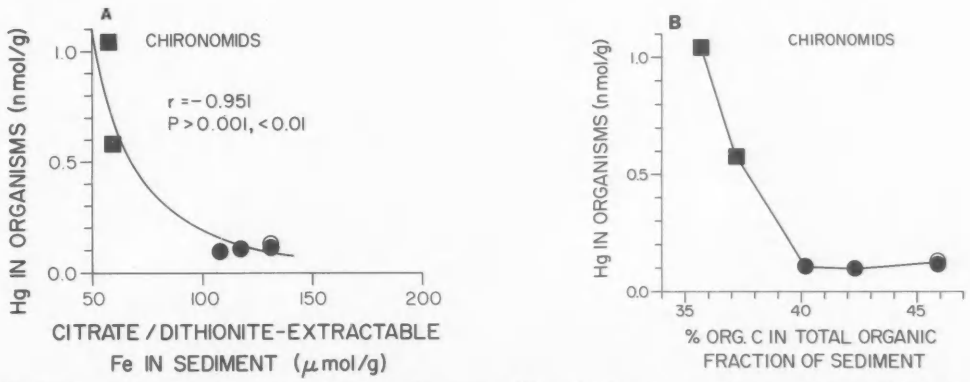

FIG. 8. Relationships between the Hg content of chironomid larvae (solid symbols) and pupae (open symbol) and (A) the citrate/dithionite-extractable Fe content of associated bottom sediment and (B) the percentage of organic C in the total organic fraction of the sediment. ■, Southern Indian Lake; ● and ○, Notigi Reservoir lakes. In the plot shown in Fig. 8B, $r = -0.841$; $0.05 > P > 0.02$.

being to some extent obscured, however, by effects of local conditions. The low Hg values for Rat Lake and South Bay probably indicate that the biological uptake of Hg was impeded by suspended clay and silt. South Bay has an anomalously great abundance of suspended fine-grained mineral detritus owing to erosion of shoreline deposits of Pleistocene glaciolacustrine silty clay, and Rat Lake is the receiving basin for turbid water flowing out of South Bay (Newbury et al. 1984; Jackson 1988b). The suspended clay and silt may interfere with the bioaccumulation of Hg by scavenging and immobilizing dissolved Hg species in the water, thereby making them less available for biological uptake, and by inhibiting microbial methylation of Hg in the sediments (not only by adsorbing Hg but also by diluting and burying organic nutrient substrates); there is also evidence that this material actively promotes demethylation of CH_3Hg^+ (Jackson 1987, 1988a, 1988b). Furthermore, the clay and silt, being poor in Hg compared with most of the lake muds in the region (compare Hecky et al. 1987 (table 2 and "Errata") and Jackson 1988b (table 9)), probably dilute and rapidly bury the more Hg-rich particulate matter being deposited on the bot-

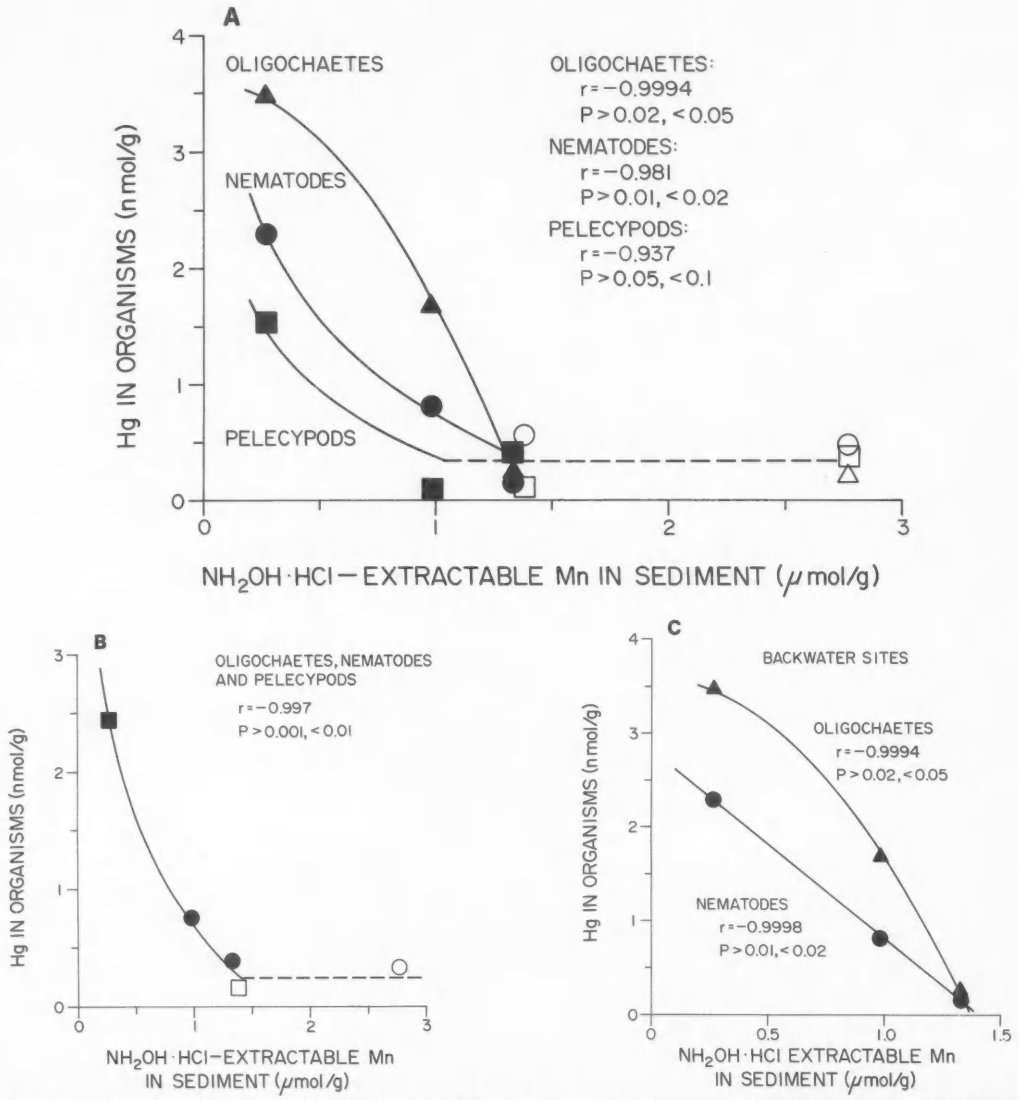

FIG. 9. Relationships between Hg concentrations in oligochaetes, nematodes, and pelecypods and the NH_2OH·HCl-extractable Mn content of the associated bottom sediment. (A) Individual plots for oligochaetes (▲,△), nematodes (●, ○), and pelecypods (■, □) from all sites; solid symbols, backwater sites; open symbols, mainstream sites. (B) Plot employing weighted average Hg concentration of combined oligochaetes, nematodes, and pelecypods from each site; ■, □, Southern Indian Lake; ●, ○, Notigi Reservoir lakes; solid symbols, backwater sites; open symbols, mainstream sites. (C) Plots for oligochaetes (▲) and nematodes (●) in backwater sites. Regression analyses and curves in Fig. 9A and 9B represent all sampling sites except Rat Lake, which is represented by the symbols on the far right. Broken lines connecting the symbols for Rat Lake with the regression curves indicate levelling off of the curves at higher Mn concentrations.

tom, thereby hindering the release of Hg from the sediments to the water column.

The hypothesis that clay and silt eroded from shoreline deposits interfere with the uptake of Hg by plankton is strongly supported by Fig. 6A and 6B, which demonstrate that the Hg concentrations in >10 μm plankton and bottom sediment are inversely related to the dolomite content of the sediment. Dolomite is a major component of the Pleistocene silty clay deposits in the field area and is unlikely to have been derived from any other source; therefore, it is an excellent marker mineral for tracing eroded, redeposited Pleistocene glacial or glaciolacustrine sediment in the rivers and lakes of the region (Jackson 1988b). The anomalously high concentration of eroded silty clay in South Bay is clearly shown in Fig. 6. (The only other anomaly is an aberrantly high concentration of Hg with respect to dolomite in sediment from East Mynarski Lake (Jackson 1988b, tables 5, 9). Compared with the other lakes in the study area, East Mynarski Lake also has an anomalously high level of primary productivity and anomalously high concentrations of sulfide in its sediments (Jackson 1988b). In view of the

TABLE 5. Correlation matrix relating the Hg content of benthic invertebrates and different physicochemical characteristics of their environment to the depth of water at the sampling site. The environmental variables represent all sampling regions except Granville Lake and the west basin of Notigi Lake (see text). All data represent samples collected in June 1981.

	Depth of water	
	r	*P*
Hg in chironomids	−0.940	>0.01, <0.02
Hg in oligochaetes	−0.919	>0.05, <0.1
Hg in nematodes	−0.811	>0.05, <0.1
Hg in pelecypods	−0.531	>>0.1
Temperature of water at bottom	−0.968	>0.001, <0.01
Citrate/dithionite-extractable Fe in sediment	0.987	<0.001
%C in total organic fraction of sediment	0.978	<0.001
NH_2OH·HCl-extractable Mn in sediment	0.588	>>0.1

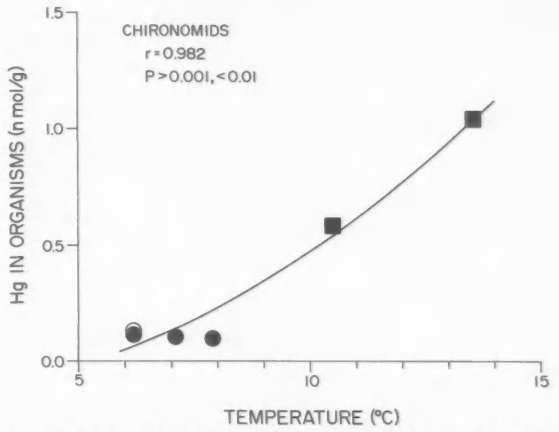

FIG. 10. Relationship between the Hg content of chironomids and the temperature of the bottom water in June 1981. Explanation of symbols same as in Fig. 8.

strong tendency of organic matter and sulfide to bind and accumulate Hg, the relatively large concentration of Hg in the sediment of East Mynarski Lake is undoubtedly a result of the high rate at which organic matter and sulfide accumulate in that particular lake.)

As with the >10 μm plankton, the geographical pattern of variation in the Hg levels of the >73 μm plankton was radically different in August than in June, although the >10 μm and >73 μm plankton fractions collected in August differed greatly from each other. The Hg concentrations in all but one of the >73 μm zooplankton samples collected in August gave a strong inverse correlation with the organic C content of the sediment (Fig. 7). Virtually the same results were obtained when Hg in plankton was plotted against the organic C content of whole or centrifuged surface water. The aberrant sampling site was South Bay, where the Hg concentration in plankton was anomalously low. The most Hg-rich plankton samples came from Granville Lake, which has not been affected by hydroelectric development, whereas the plankton from Central Mynarski Lake, where impoundment caused a 6.9-m rise in lake level, had the second lowest Hg concentration.

The negative correlation between Hg in zooplankton and organic C in sediments and water can be ascribed to reduced bioavailability of Hg resulting from the binding of dissolved Hg by humic matter and other organic complexing agents. Note that the highest organic C concentrations in sediments and the lowest Hg levels in zooplankton occurred in backwater regions, where autochthonous humic matter leached from local forest soils and muskeg is most highly concentrated. The aberrantly low Hg content of South Bay zooplankton can probably be explained by suppression of the bioaccumulation of Hg due to the anomalously great abundance of eroded shoreline clay and silt at that particular site.

The marked seasonal differences between the geographical variations in the Hg content of plankton in the lakes of the study area cannot be explained without additional information, but the most likely reason would seem to be seasonal changes in the physical conditions in the water column. In June, when the spring flood was in progress, there was relatively vigorous flushing by river currents and therefore diminished influence of local environmental conditions. In August, when river flow had slackened, local conditions probably had a much stronger effect on the plankton.

Benthic Invertebrates

As with plankton other than the >10 μm plankton collected in August, Hg levels in benthic chironomids, oligochaetes, nematodes, and pelecypods were not significantly related to Hg levels and methylation rates in their immediate surroundings (Tables 3, 4). Hg concentrations in all four types of benthic invertebrate consistently gave highly insignificant correlations ($P > 0.1$) with the CH_3Hg^+, total Hg, and $CaCl_2$-extractable Hg concentrations of the sediment and with the Hg methylating capability of the sediment, and 75% of the correlation coefficients were negative (Table 4).

Surprisingly, the highest Hg concentrations in benthic invertebrates occurred in Southern Indian Lake rather than Notigi Reservoir lakes (Table 3) whereas the distribution of total Hg, CH_3Hg^+, and "available inorganic Hg" concentrations and relative rates of Hg methylation in the bottom sediments (not counting aberrantly low total Hg levels in samples collected from the west basin of Notigi Lake in 1981 (Jackson 1988b)) would lead one to expect the reverse of that result. Furthermore, Hg data for different invertebrate taxa differed systematically among themselves, both in absolute value and in their geographical distribution. These findings imply that the net rates of Hg accumulation by benthic invertebrates were more strongly influenced by certain environmental and biological processes than by the abundance of the CH_3Hg^+ or inorganic Hg species in their habitat. As discussed below, the concentrations of Hg in the organisms appear to be determined largely by the composition of the sediment, although ambient temperature may also play a role. Specific biological factors such as feeding habits must be taken into account as well.

Hg levels in benthic animals correlated inversely with the concentrations of hydrated Fe and Mn oxides and C-rich humic matter in the bottom sediment. The Hg content of chironomids decreased logarithmically with increasing concentrations of citrate/dithionite-extractable Fe in the sediments (Fig. 8A) and with increasing abundance of C in the organic fraction of the sediment (Fig. 8B), levelling off at higher Fe and organic C concentrations. These variables are highly dependent on the

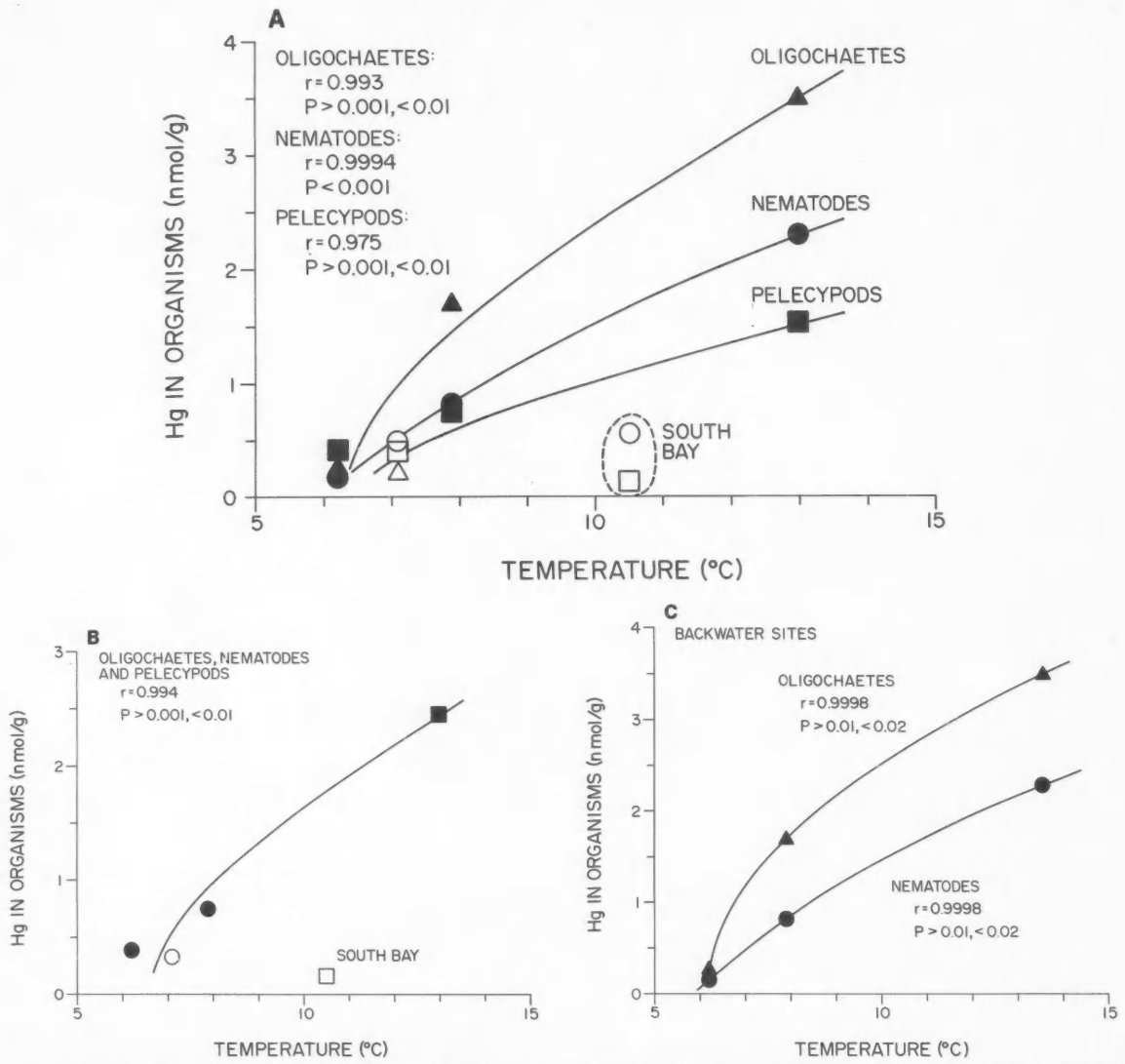

FIG. 11. Relationships between Hg concentrations in oligochaetes, nematodes, and pelecypods and the temperature of the bottom water. (A) Individual plots for oligochaetes, nematodes, and pelecypods from all sites. (B) Plot employing weighted average Hg concentration of combined oligochaetes, nematodes, and pelecypods from each site. (C) Plots for oligochaetes and nematodes in backwater sites. Regression analyses and curves in Fig. 11A and 11B represent all sampling sites except South Bay. Explanation of symbols same as in Fig. 9.

depth of water, the abundance of Fe oxide and C increasing with depth while the Hg concentrations in chironomids decrease (Table 5). (*Note*: The relationship between the Hg content of the organisms and the nature of the sedimentary organic matter has also been commented upon by W. F. Warwick (unpubl. data).)

In contrast with the Hg content of chironomids, the Hg concentrations in oligochaetes, nematodes, and pelecypods varied inversely with the $NH_2OH \cdot HCl$-extractable Mn content of the sediment, levelling off sharply at Mn concentrations greater than about 1.3 μmol/g (Fig. 9A, 9B). Also note that the correlation of these variables with depth of water is relatively weak (Table 5). Furthermore, there is a clear-cut separation between the Mn-rich mainstream regions and the Mn-poor backwater regions, the significant correlation between Hg and Mn being confined to the backwater zone (Fig. 9A). In the more Mn-rich environments, in which the Hg levels in the organisms were minimal, the three types of invertebrates differed only slightly in Hg content; but in Mn-poor environments, where Hg levels were high, they differed considerably, the Hg levels decreasing in the order oligochaetes > nematodes > pelecypods (Fig. 9A, 9C). In Fig. 9A the regression curves for nematodes and pelecypods are similar in shape but differ markedly from the curve for oligochaetes, suggesting that the Hg uptake kinetics are different in oligochaetes than in the other organisms.

TABLE 6. Estimates of total biomass of benthic macroinvertebrates at different sampling sites (computed from data supplied by W. F. Warwick (pers. comm. and unpubl. data)).

Sampling site	Total biomass (g/m^2)
Southern Indian Lake	
Long Bay (shallow cove)	1.504
South Bay	6.092
Notigi Reservoir	
Rat Lake	52.894
Central Mynarski Lake	42.520
Notigi Lake (east basin)	7.513

TABLE 7. Correlation matrix relating Hg concentrations in different benthic invertebrate groups to the total biomass of the benthic macroinvertebrate community.

	Total biomass of macroinvertebrate community	
	r	P
Hg in chironomids	−0.872	>0.05, <0.1
Hg in oligochaetes	−0.674	>>0.1
Hg in nematodes	−0.618	>>0.1
Hg in pelecypods	−0.720	>>0.1

The systematic differences between oligochaetes, nematodes, and pelecypods may reflect differences in feeding habits. An oligochaete typically passes huge quantities of mud through its gut when feeding (Clegg 1974; Pennak 1978), and this probably results in rapid assimilation of available forms of Hg from ingested sediment particles. In contrast, nematodes as a whole have a wide range of feeding habits and feed on a variety of living and nonliving organic materials, only some of which are scavenged from bottom sediments (Crofton 1966; Pennak 1978), while pelecypods are filter feeders which consume suspended organic particles from the water column and even winnow inedible sediment particles out of their food (Clegg 1974; Pennak 1978). Thus, the intake of bottom sediment by the organisms, like the concentrations of Hg in their bodies, presumably diminished in the order oligochaetes > nematodes > pelecypods, suggesting a correlation between the quantity of fine-grained sediment consumed and the amount of Hg assimilated in a given period of time. Such a correlation would be a natural consequence of the fact that the finer-grained bottom sediments are enriched in Hg with respect to the overlying water (Jackson 1988b, tables 9, 10). On the other hand, a cautionary note would be appropriate: the Hg data for oligochaetes, nematodes, and pelecypods are subject to an unknown degree of error because (1) the gut contents could not be voided prior to chemical analysis and (2) the weights of the pelecypod specimens included the shell weights.

The extractable sedimentary Fe and Mn fractions which correlate inversely with Hg levels in benthic invertebrates are thought to represent collodial hydrated oxides, here symbolized as FeOOH and MnOOH (see references in Jackson 1988b, table 2). However, the FeOOH was associated with sedimentary humic matter as represented by brown organic substances extracted with 0.1 M NaOH. Thus, the citrate/dithionite-extractable Fe gave strong positive correlations with the colour (absorbance at 465 nm) of NaOH extracts of the sediments (for June samples, $r = 0.967$; $P < 0.001$) and with NaOH-extractable organic C (for June samples, $r = 0.926$; $P < 0.001$) (see data in Jackson 1988b, tables 7, 13). The FeOOH was probably complexed with humic substances, which have a strong affinity for hydrated ferric oxides and Fe(III) in general (Schnitzer and Khan 1972). The percentage of C in the organic matter is interpreted as an approximate measure of the proportion of allochthonous (land-derived) humic matter in the organic fraction of the sediment. This interpretation is based on the following facts:

(1) The %C values for the organic matter in sediments collected in June (with the exception of samples from Granville Lake and the west basin of Notigi Lake) gave significant positive correlations with the concentrations of NaOH-extractable colour ($r = 0.962$; $0.01 > P > 0.001$) and NaOH-extractable organic C ($r = 0.894$; $0.02 > P > 0.01$) in the sediments. (Granville Lake and west Notigi Lake sediments, which had aberrantly low values of %C and had a number of other anomalies in common (Jackson 1988b), gave a separate but parallel trend. Possibly the reason for the anomaly is that the sampling regions in Granville Lake and west Notigi Lake, being located in zones of exceptionally vigorous fluvial current action, had relatively low concentrations of humic matter derived from local soils and muskeg, and thus had proportionately larger amounts of riverborne humic matter transported from further upstream.) Coloured organic substances extracted from sediment or soil with alkali consist principally of humic matter, and the colour intensity and C content of the extract tend to increase with both the concentration of humic matter in solution *and* the humic matter's degree of humification, or maturity (degree of "humic" as opposed to "fulvic" character) (Schnitzer and Khan 1972).

(2) Allochthonous humic matter formed from remains of land plants and other terrestrial organisms generally tends to be more mature, and hence more C rich, than is autochthonous humic matter derived from aquatic organisms (Jackson 1975).

(3) In northern Manitoba the sediments from the backwater zone of Notigi Reservoir, where the influence of local drainage from highly humic forest soil and muskeg is particularly great (see data in Jackson 1988b, tables 4, 11), had the most C-rich organic matter. (However, the meaning of this relationship is ambiguous because the %C values were also strongly correlated with depth of water, the depth being greater at the Notigi Reservoir sites than at the Southern Indian Lake sites (Table 5).)

The relationships illustrated in Fig. 8 and 9 suggest that the binding of Hg species by FeOOH and MnOOH, and possibly by higher molecular weight humic substances, reduces the availability of Hg to benthic animals, thereby limiting their rate of Hg accumulation. It has been demonstrated that hydrated oxides and organic matter may interfere with the accumulation of heavy metals by freshwater molluscs (Tessier et al. 1984) and rainbow trout fry (*Salmo gairdneri*) (T. A. Jackson, unpubl. data and manuscr. in preparation), and the same principles could very well apply in the present case. Morever, higher molecular weight humic fractions of sediments bind Hg preferentially with respect to lower molecular weight fractions (Jackson et al. 1980).

This provisional interpretation of the results shown in Fig. 8 and 9 implies that chironomids accumulate certain chemical species of Hg more readily than do the oligochaetes, nematodes, and pelecypods and that these Hg species are also preferentially adsorbed by FeOOH or humic acid, or FeOOH–humic complexes, whereas the other three invertebrate groups preferentially accumulate other forms of Hg that happen to be preferentially adsorbed by MnOOH. Although further research is

needed to confirm it, this hypothesis is reasonable because of the following considerations: (1) the Hg accumulated by invertebrates, unlike Hg in fish tissue, commonly has a high proportion of nonmethyl, or inorganic, Hg (Huckabee et al. 1979; Windom and Kendall 1979; T. A. Jackson, unpubl. data and manuscr. in preparation), which could comprise a variety of chemical species, such as soluble complexes, that differ in their affinities for adsorption sites on sedimentary particles and in their availability for uptake by organisms; and (2) hydrated Fe and Mn oxides in Mn nodules are known to have different trace-metal preferences (Burns and Fuerstenau 1966; Calvert and Price 1977) and therefore could conceivably discriminate between different chemical species of Hg.

Ambient temperature may also have influenced the accumulation of Hg by the benthic invertebrates. Thus, Hg levels in chironomids and oligochaetes gave strong positive correlations with water temperature at or near the sediment–water interface (Fig. 10, 11A). Hg concentrations in nematodes and pelecypods, however, gave relatively weak positive correlations with temperature because the specimens from South Bay were anomalously low in Hg with respect to temperature; strong correlations were obtained only if the data for South Bay were disregarded (Fig. 11A, 11B). Actually, the plot for oligochaetes is not strictly comparable with the plots for nematodes, pelecypods, and chironomids because no oligochaetes were found in South Bay. Nevertheless, the previously discussed biogeochemical kinship between oligochaetes, nematodes, and pelecypods as contrasted with chironomids (Fig. 8A, 8B, 9A) is sufficient grounds for surmising that if a complete set of Hg data were available for oligochaetes, they would show essentially the same pattern of variation as the data for nematodes and pelecypods.

At backwater sites, oligochaetes were consistently richer in Hg than were nematodes (Fig. 11C), as discussed above, and their respective regression lines diverge with increasing temperature, although the correlation coefficients and significance probabilities for the two curves are identical. The Hg levels in backwater faunas correlate as strongly with temperature as with $NH_2OH{\cdot}HCl$-extractable Mn or even more strongly; however, in the plots of Hg against temperature (Fig. 11), unlike the plots of Hg against $NH_2OH{\cdot}HCl$-extractable Mn (Fig. 9), there seems to be no logical basis for treating backwater and mainstream samples as separate subgroups.

As the results illustrated in Fig. 10 and 11 demonstrate, a direct effect of temperature on the uptake of Hg by invertebrates is a distinct possibility. From a physiological standpoint this is plausible, as other studies have established that rates of Hg bioaccumulation in at least some aquatic organisms increase with temperature owing to enhancement of metabolic rates (MacLeod and Pessah 1972; Burkett 1974; Shin and Krenkel 1976). The aberrantly low Hg levels in organisms from South Bay (Fig. 11A, 11B) could be attributed to diminished bioavailability of Hg due to the scavenging of Hg by the massive quantities of clay and silt being introduced into the bay as a result of shoreline erosion (cf. Fig. 4B, 6A, 6B, 7). On the other hand, this aberration did not occur in the chironomid data (Fig. 10).

A third interpretation of the data for benthic invertebrates has been proposed by W. F. Warwick (unpubl. data and pers. comm.). Noting that the total invertebrate biomass (mass of organisms per unit area of lake bottom) tended to be greater in Notigi Reservoir lakes than in Southern Indian Lake (Table 6), Warwick postulated that the paradoxical occurrence of low Hg levels in the Notigi Reservoir fauna and high Hg levels in the Southern Indian Lake faunas resulted from biodilution of the Hg (cf. Jernelöv et al. 1975). This hypothesis, however, does not stand up well under scrutiny. Regression analysis relating the Hg concentrations in the organisms to the total biomass of the macroinvertebrate community at each site yielded negative correlation coefficients as predicted by the biodilution theory, but all four of the correlations are insignificant (Table 7). (Besides, at least a small part of each correlation is attributable to self-correlation.) Thus, biodilution appears to play only a very trifling role, if any.

The question now arises whether the observed variations in the Hg concentrations in benthic invertebrates can be better explained by the distribution of hydrated oxides and humic matter in the sediment or by variations in ambient temperature. Both interpretations are plausible, and, as they are not mutually exclusive, both could well be correct; but further research, including controlled experiments as well as field studies, would be needed to disentangle the cause-and-effect relationships. The data for chironomids are particularly ambiguous, as they are all strongly dependent on depth of water and therefore correlate significantly with each other.

Nevertheless, it would seem that the suggested inhibitory effect of FeOOH, MnOOH, and humic matter on the biological uptake of Hg can best account for the available data as a whole. In the graph relating Hg levels in nematodes and pelecypods to ambient temperature, the data for South Bay are definitely aberrant (Fig. 11A) whereas no such anomaly exists in the plots of Hg level against $NH_2OH{\cdot}HCl$-extractable Mn. This favours the idea that adsorption of Hg by MnOOH was the principal limiting factor controlling the rate at which the organisms accumulated Hg. Another argument in favour of this hypothesis arises from the relationships between the Hg concentrations in the organisms and the depth of water at the sampling sites (Table 5). Pelecypods gave by far the poorest correlation (the only highly insignificant relationship ($P >> 0.1$)) and pelecypods are also the only organisms among the four groups investigated which specialize in filter feeding and actively exclude sediment particles. All three other groups either specialize in deposit feeding or include deposit-feeding species. This pattern of variation suggests that the depth-related factor which controlled the uptake of Hg by the animals was the nature of the ingested sediment — for instance, the abundance of FeOOH, MnOOH, and humic matter — not the temperature.

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Freshwater Zooplankton Community Structure: Introduction of Large Invertebrate Predators and Large Herbivores to a Small-Species Community

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Two hypotheses have been proposed to explain the scarcity of small zooplankton species in fishless lakes, in which large zooplankton species dominate: (1) selective predation on small species by large invertebrate predators and (2) competitive suppression of small species by large herbivores. These hypotheses were tested at the Experimental Lakes Area (ELA) by introducing a large invertebrate predator, *Chaoborus americanus*, and a large herbivore, *Daphnia catawba*, both common in fishless ELA lakes, into a zooplankton community typical of ELA lakes with fish (small zooplankton species present). *Chaoborus* had much more of an impact than *D. catawba* on resident zooplankton, although both introduced species significantly reduced the abundance of some resident species. *Daphnia galeata mendotae*, the dominant species in the absence of introduced species, was reduced to virtual extinction by *Chaoborus*. The cladocerans *Bosmina* and *Diaphanosoma*, the copepods *Diaptomus* spp., and the rotifer *Conochilus* also were reduced in abundance by *Chaoborus*. *Daphnia galeata mendotae* and *Bosmina* were the only resident species consistently reduced in abundance by *D. catawba*. These results support current conceptual models that depict invertebrate predation as an important factor responsible for the relative scarcity of small zooplankton species in fishless lakes.

On a avancé deux hypothèses pour expliquer la rareté de petites espèces de zooplancton dans des lacs dépourvus de poisson, où dominent de grosses espèces de zooplancton : 1) la prédation sélective exercée sur de petites espèces par de gros invertébrés et 2) la concurrence des gros herbivores. Ces hypothèses ont été vérifiées dans la Région des lacs expérimentaux (RLE), par l'introduction d'un gros prédateur invertébré, *Chaoborus americanus*, et d'un gros herbivore, *Daphnia catawba*, tous deux répandus dans les lacs de la RLE dépourvus de poisson, dans une communauté zooplanctonique typique des lacs de la RLE contenant du poisson (petites espèces de zooplancton présentes). L'espèce *Chaoborus* a eu beaucoup plus d'influence que *D. catawba* sur le zooplancton résidant, bien que les deux espèces introduites aient réduit de façon significative l'abondance de certaines espèces résidantes. *Daphnia galeata mendotae*, qui est l'espèce dominante en l'absence des espèces introduites, a été pratiquement réduite à l'extinction par *Chaoborus*. L'abondance des cladocères *Bosmina* et *Diaphnanosoma*, des copépodes *Diaptomus* spp. et du rotifère *Conochilus* a été réduite par *Chaoborus*. *Daphnia galeata mendotae* et *Bosmina* ont été les seules espèces résidantes dont l'abondance a été réduite de façon constante par *D. catawba*. Ces résultats étayent les modèles conceptuels actuels qui décrivent la prédation par les invertébrés comme un facteur important responsable de la rareté relative de petites espèces de zooplancton dans des lacs dépourvus de poisson.

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Freshwater zooplankton communities exhibit a relatively predictable pattern according to the presence of fish or other vertebrate predators (e.g. Hrbáček 1962; Brooks and Dodson 1965; Zaret 1980). Lakes with abundant planktivorous fish are dominated by small-bodied zooplankton species; larger species are eliminated by size-selective fish predation. Lakes with few or no fish are usually dominated by large zooplankton species, including herbivores and predators. Small species are generally rare or absent in such lakes.

Two hypotheses have been proposed to account for the general scarcity of small zooplankton species in fishless lakes. One is that large herbivores competitively reduce the abundance of small species (Brooks and Dodson 1965). A second hypothesis is that large invertebrate predators reduce the abundance of small species by selectively preying on them (Dodson 1974). Alternatively, the scarcity of small zooplankton species in the presence of large species may be due to a combination of both competition and predation. Current conceptual models favor the predation hypothesis (Zaret 1980), but recent experimental results suggest that competitive suppression by large herbivores can reduce the abundance of small species (Smith and Cooper 1982; DeMott and Kerfoot 1982; Neill 1984; Gilbert and Stemberger 1985; Vanni 1986). Only one study has explicitly tested the two hypotheses on a community-level scale. Based on a relatively short-term, small-container experiment in alpine

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ponds, Dodson (1974) concluded that invertebrate predation was responsible for the scarcity of small species in fishless ponds, while competition was unimportant.

In this paper I report the results of a replicated field experiment that addressed the potential importance of competition and invertebrate predation in structuring zooplankton communities. To do so, a small-species zooplankton community typical of a lake with abundant planktivorous fish was isolated from its fish predators in in situ enclosures. Large herbivores and large invertebrate predators, typical of fishless lakes, were then added to this community, simulating what may happen if planktivorous fish were in fact excluded from the lake. The effects of the introduced species provide a measure of the potential effects of invertebrate predation and competition on zooplankton community structure. This approach is similar to that of Dodson (1974), but on a larger spatial and temporal scale.

Study Area

This experiment was conducted in Lake 221, a small, shallow lake (surface area 8 ha, maximum depth 5.5 m) within the Experimental Lakes Area (ELA) in northwestern Ontario (for specific location see Johnson and Vallentyne 1971). The area lies within the Precambrian Shield, with typical boreal forest vegetation (Brunskill and Schindler 1971). Lake 221 is oligotrophic and the phytoplankton community is dominated by green algae and chrysophytes. Only two fish species are present: yellow perch (*Perca flavescens*) and pearl dace (*Semolitus margarita*). Small perch are numerous compared with other ELA lakes (K. Mills, Freshwater Institute, Winnipeg, Man., pers. comm.) and are planktivorous (M. Vanni and K. Mills, unpubl. data). During this experiment (1985), the lake zooplankton community was dominated by the copepods *Diaptomus minutus* and *Diaptomus oregonensis*, the cladocerans *Daphnia galeata mendotae*, *Holopedium gibberum*, and *Bosmina longirostris*, and several rotifer species.

The carapace length of *Daphnia* is often used as an indicator of planktivorous fish predation intensity in lakes (Zaret 1980). The *D. galeata mendotae* of Lake 221 are generally of small body size compared with other *D. galeata mendotae* populations. Even upon excluding fish, Lake 221 *D. galeata mendotae* rarely reach a carapace length >1.5 mm (see Results), while this species often attains a carapace length >2 mm in other ELA lakes (Lawrence et al. 1988) and in Lake Mendota, its type locality (M. Vanni, unpubl. data). Thus although some authors have considered *D. galeata mendotae* to be a large daphnid (Brooks and Dodson 1965), in Lake 221 this species is of intermediate size relative to other North American daphnids, indicating that planktivorous fish density is also intermediate relative to other lakes (Zaret 1980).

Data on the zooplankton of fishless ELA lakes is scant, particularly data on *Chaoborus* distributions. Of 15 lakes sampled by Hamilton (1971) for chaoborids, only two were known to be fishless at the time of sampling (Beamish et al. 1976; D. W. Schindler, Freshwater Institute, Winnipeg, Man., pers. comm.). Data from limited sampling of three additional fishless lakes (M. Vanni, unpubl. data) and other lakes sampled by Hamilton (1971) for chaoborids, Beamish et al. (1976) for fishes, and Patalas (1971) for crustacean zooplankton yield some general patterns (Table 1). *Chaoborus americanus* is confined to fishless ELA lakes, in agreement with von Ende's (1979) study of Michigan lakes. Fishless ELA lakes are inhabited by relatively large *Daphnia* species (*D. catawba* and *D. schoedleri*); the largest North American lake daphnids (e.g. *D. pulex* and *D. pulicaria*) are exceedingly rare in ELA lakes (Patalas 1971). Lakes with fish are inhabited by smaller chaoborids and smaller daphnids; *D. galeata mendotae* is the dom-

TABLE 1. Distribution of *Chaoborus* and *Daphnia* species in ELA lakes in relation to fish distributions.

Lake	Dominant fish species[a]	*C. americanus* (present/absent)[b]	Other *Chaoborus* species[b]	Dominant *Daphnia* species[c]
81	Fish absent[d]	+	*C. brunskilli*	*D. schoedleri*
230	Fish absent	+	*C. brunskilli*, *C. punctipennis*, *C. flavicans*	*D. schoedleri*
304	Fish absent[d]	+[e]	*C. trivitattus*[e]	None[e]
225	Fish absent	−[e]	None[e]	*D. catawba*[e]
679	Fish absent	+[e]	Unknown	*D. catawba*, *D. galeata mendotae*
161	Yellow perch, lake trout	−	None	*D. galeata mendotae*
239	Yellow perch	−	*C. punctipennis*	*D. galeata mendotae*
240	Yellow perch	−	*C. punctipennis*	*D. galeata mendotae*
305	Yellow perch, lake trout	−	*C. punctipennis*	*D. galeata mendotae*
221	Yellow perch, pearl dace	−[e]	*C. punctipennis*[e]	*D. galeata mendotae*[e]
122	Pearl dace	−	*C. punctipennis*, *C. flavicans*	*D. galeata mendotae*
227	Pearl dace, redbelly dace	−	*C. punctipennis*, *C. flavicans*	*D. retrocurva*
304	Fathead minnow, pearl dace, redbelly dace	−	*C. punctipennis*	None; *Diaphanosoma*, *Bosmina*
132	Fathead minnow	−	*C. flavicans*	None; *Diaphanosoma*, *Bosmina*

[a]All fish species listed as "abundant" by Beamish et al. (1976), excluding those unlikely to be planktivorous (i.e. sucker, sculpin).

[b]From Hamilton (1971), except as noted.

[c]From Patalas (1971), except as noted.

[d]Not sampled by Beamish et al. (1976). Fish were absent in Lake 81 at the time it was sampled by Hamilton (1971) and Patalas (1971) (D. W. Schindler, pers. comm.) and in Lake 304 at the time of the present study (K. Mills, pers. comm.).

[e]M. Vanni (this study and unpubl. data)

inant daphnid in lakes with yellow perch as the dominant fish species, while *D. retrocurva* or smaller nondaphnid cladocerans prevail in lakes in which minnows are the dominant fish species (Table 1).

Materials and Methods

Experimental Design

I examined the potential importance of competition and predation by introducing a large invertebrate predator, *C. americanus*, and a relatively large herbivore, *D. catawba*, both common in fishless ELA lakes, to the resident Lake 221 zooplankton community contained within experimental enclosures. The rationale behind this approach is that if planktivorous fish were removed or greatly reduced in abundance in a lake, these large species would colonize the lake. Therefore, the potential effects of these large species can be assessed by introducing them into a zooplankton community dominated by species of small and intermediate size, i.e. a community typical of lakes with relatively abundant planktivorous fish. This study represents the first attempt to address both the predation and competition hypotheses in a large-scale, long-term (i.e. several zooplankton generations) experiment and represents an expansion of the early experiments of Dodson (1974).

I employed four treatments in this experiment: (1) Control, with natural densities of resident Lake 221 plankton; (2) *C. americanus* added to enclosures along with resident plankton; (3) *D. catawba* added to enclosures along with resident plankton; and (4) *C. americanus* and *D. catawba* both added to enclosures. All treatments excluded fish. Each treatment was initiated in triplicate, for a total of 12 enclosures. This design allowed for detection of the effects of each of the two invading species, as well as their interaction, on the dynamics of the relatively small species that reside in Lake 221.

Enclosures were made of translucent woven polyethylene. Each enclosure was a cylinder 2 m in diameter and 3.25 m deep, yielding a volume of ~10 000 L. Ribs made of ABS plastic were fastened to each enclosure at its top, middle, and bottom (on the outside wall) to provide structural support. Enclosures had polyethylene bottoms, completely isolating their contents from lake water. Enclosures were suspended by wooden and styrofoam frames. Frames were anchored in place in the deepest area of Lake 221 in late June 1985. On 3 July, each enclosure was lowered in a collapsed form to ~3.25 m depth by two SCUBA divers. The divers then slowly raised the enclosure top to the lake surface underneath the frames, with the help of two people at the surface pulling on ropes attached to the top rib of the enclosure. The bottom of the enclosure remained at ~3.25 m. Each enclosure top was then fastened to the frame. Four enclosures were attached to each frame. Before the above process was undertaken, a coarse nylon mesh was placed over the top of each enclosure so that fish would not be trapped in the enclosures as they were raised to the surface. This mesh was kept in place during the experiment, except during sampling, to prevent fish from jumping into the enclosures. The above procedure filled the enclosures to ~80% capacity. The enclosures were filled to capacity on 4 July with a gasoline-powered pump.

Chaoborus americanus individuals were collected on 9 July from Lake 304, a fishless ELA lake in which *C. americanus* is abundant, with a coarse mesh net which trapped *Chaoborus* but not crustaceans or rotifers. Other large invertebrates, e.g. notonectids, were removed from the sample in the field. *Chaoborus* individuals were then put in 3.8-L jars filled with screened (53-μm mesh) Lakes 304 water and transported to a laboratory at the ELA field station. *Chaoborus* were then concentrated with a Nitex screen and placed in a large plastic tub containing filtered (53-μm mesh) Lake 221 water which had been collected the previous evening. The *Chaoborus* population was then mixed thoroughly in the tub and subsampled to determine the number of individuals therein. Previous subsampling had shown that the coefficient of variation (SD/mean) among subsamples was <3% using this method. Aliquots of the *Chaoborus* population were then transferred to each of six 3.8-L jars, transported to Lake 221 that evening and added to each of the six enclosures designated to receive *Chaoborus*. The entire process was repeated on 10 July. In total, ~3000 *Chaoborus* individuals were added to each enclosure, for a density of ~0.3/L. *Chaoborus americanus* density in Lake 304, the source lake, was 0.35/L at this time (M. Vanni, unpubl. data). Additional *Chaoborus* were introduced from Lake 304 to Lake 221 enclosures, in the above manner, on 6 August (400 ind./enclosure) and 2 September (300 ind./enclosure) to replace individuals removed by sampling. No other zooplankton species were inadvertently transferred from lake 304 to Lake 221 enclosures, and placement of the *Chaoborus* in Lake 221 water before transferring them to enclosures minimized the possibility of contamination with Lake 304 phytoplankton.

Daphnia catawba individuals were collected on 16 July from Lake 225, a fishless ELA lake in which *D. catawba* is abundant, with the same net used to collect *Chaoborus*. This net also trapped *H. gibberum* from Lake 225, but no other zooplankton species. *Daphnia catawba* individuals were placed in 3.8-L jars in screened (53-μm mesh) Lake 225 water and transported to a laboratory at the ELA station, where they were concentrated and then diluted in screened (53-μm mesh) Lake 221 water. This process also transferred *Holopedium* from Lake 225; therefore the aliquot method used for *Chaoborus* could not be used for *D. catawba*. Instead, *D. catawba* individuals were captured 1–10 at a time with a wide-mouth pipette. Individuals were counted as they entered the pipette and transferred to each of six jars containing filtered Lake 221 water. *Daphnia catawba* were transported to Lake 221 that evening and added to the six enclosures designated to receive *D. catawba*. Five hundred individuals were added to each enclosure on 16 July, and 500 more individuals were added on 17 July using the same procedure. The initial density, ~0.1/L, represents a low density and allowed the *D. catawba* population to expand as it might following colonization of a fish-free Lake 221.

The densities of *Chaoborus* and *D. catawba* were realistic for fishless ELA lakes, as mentioned above, and certainly within the range of fishless lakes in general. The two species were introduced into Lake 221 enclosures to simulate their colonization following removal of planktivorous fish. The objective was to allow the two "exotic" species to achieve realistic, stable population densities (as they would following colonization) as quickly as possible, rather than monitor their effects as they increased in density. This was accomplished easily with *Chaoborus* because a large number of individuals could be sorted and transferred. Furthermore, adding *Chaoborus* at a density similar to that in the source lake is valid because the experimental population was likely to maintain this density or decline due to mortality and/or emergence, as it would in the source lake. Recruitment of young *C. americanus*

into the enclosures was unlikely. In addition to being similar to source Lake 304, the densities of *Chaoborous* in this experiment were well within the range found in fishless lakes elsewhere. The densities in this experiment were higher than those found for *Chaoborus trivitattus* by Neill (1981), but up to an order of magnitude lower than *C. americanus* densities found by others in fishless habitats (Dodson 1974; Lynch 1979; von Ende 1979). Introduction of *D. catawba* was more problematic. It was difficult to separate large numbers of *D. catawba* from *Holopedium* in Lake 225 water. Furthermore, *D. catawba* was likely to reproduce and expand in numbers in the enclosures (Vanni 1986), and selecting and achieving a "target" density was therefore arbitrary. In view of these problems, I chose to introduce *D. catawba* at low densities and allow the population to increase to its carrying capacity in the enclosures. Population growth in the enclosures was indeed sigmoidal (see Results).

Two enclosures had to be discarded from the experiment. One $+D.$ *catawba* enclosure partially collapsed within a few days after filling, presumably because of a hole in its wall, and was not sampled. One enclosure in the $+C.$ *americanus* treatment had no detectable *Chaoborus* present within a few days after adding *Chaoborus*. Because *Chaoborus* survived well in the other five enclosures to which it was added, I suspected that a fish had accidentally been trapped in the enclosure in which *Chaoborus* did not survive. This suspicion was confirmed at the end of the experiment when a small (105-mm length) yellow perch was recovered from the enclosure. Although this enclosure was sampled throughout the experiment, results are not included here. Thus, for purpose of analysis, the $+D.$ *catawba* and $+C.$ *americanus* treatments were represented by two enclosures, while the other two treatments were represented by three enclosures.

Sampling Methods

Zooplankton were sampled with a device that consisted of two clear Plexiglas barrels 13 cm in diameter, each fitted with a long (~2 m) plankton net with 53-μm mesh (Chang et al. 1980). This device is towed vertically but samples most zooplankton species with an efficiency similar to that of a Schindler–Patalas trap (D. Malley, Freshwater Institute, Winnipeg, Man., pers. comm.). Vertical hauls were taken from ~3 m to the surface in each enclosure on each sampling date, collecting zooplankton from ~120 L of water, assuming 100% efficiency. Enclosures were sampled every 4–5 d in July–August and every 9–13 d in September–October. Samples were preserved in a cold sucrose–Formalin solution (Prepas 1978). All *C. americanus* individuals in the sample were counted. For all other species, three subsamples constituting up to 50% of the total sample volume were examined and all species enumerated. However, if <100 individuals of a particular species were counted before three subsamples had been enumerated, counting of that species ceased. All taxa were identified to species with the exception of *D. minutus* and *D. oregonensis* and copepod nauplii, which were not distinguished in routine counts. At the beginning and near the end to the experiment, *D. minutus* and *D. oregonensis* were counted separately to assess differential effects of the treatments on these congeners.

In addition to enumeration of individuals, eggs carried by the cladocerans *D. catawba, D. galeata mendotae,* and *B. longirostris* were counted in samples containing ≥ 50 individuals. Per capita instantaneous birth (b) and death (d) rates were estimated with the egg ratio method (Paloheimo 1974). Egg development times used in calculating b were taken from Hall (1964) for *D. galeata mendotae*, Vivjberg (1980) for *Bosmina*, and Hebert (1978) for *D. catawba* (using values for *D. pulex*).

After the *D. catawba* populations became established and attained their highest mean density (9 September), carapace body length measurements were made on 100 individuals each of *D. catawba* and *D. galeata mendotae*, using a compound microscope and an ocular micrometer, from one enclosure in the $+D.$ *catawba* treatment. Individuals were measured from the top of the eyespot to the base of the tail spine. After 100 individuals were measured, an addiitonal 50 ovigerous females were measured. These measurements were made to aid in the interpretation of the differences in the two species' abilities to coexist with the introduced *Chaoborus*.

Further measurements were made on five dates throughout the experiment, including one premanipulation date, to determine the biomass of each zooplankton species in the treatments. Measurements of all species (≤ 50 individuals) were made as in Lawrence et al. (1988). Biomass of each crustacean species was estimated from the length–weight regressions of Lawrence et al. (1988). Mean mass of rotifer species was taken from Bottrell et al. (1976) and Schindler and Noven (1971). The biomass estimates were used to calculate the proportion similarity between treatments (see Statistical Methods below). In addition, on three dates, mean herbivorous zooplankton mass was estimated by weighting the mean mass of each species by the proportion of total zooplankton individuals contributed by that species. All mean zooplankton mass estimates exclude *D. catawba* and *Chaoborus*.

In order to assess the feeding habits of *Chaoborous* in the experiment, I examined the crop contents of *Chaoborus* individuals taken from the enclosures. *Chaoborus* rapidly reduced several resident species to nearly undetectable levels; thus, prey items were too rare in *Chaoborus* enclosures to permit analysis of feeding selectivity. Therefore, on 18 October, after the experiment was terminated, I introduced ~200 *Chaoborus*, taken from Lake 304 in the same manner as earlier individuals, into one Control and one $+D.$ *catawba* enclosure, where prey items were more numerous. *Chaoborus* individuals were collected on 20 October and crops examined according to the methods of Swift and Fedorenko (1973). Although sample sizes were small (only 10–20 individuals were recovered from each enclosure), this examination provided some information on feeding habits of *Chaoborous* in the enclosures.

Phytoplankton were monitored in the enclosures on a weekly basis, except during September and October when some sampling intervals were longer. An integrated sample from 0–3 m was collected from each enclosure with Tygon tubing, preserved in Lugol's solution, settled, and examined using an inverted microscope. Enclosure water temperature was monitored at 1-m intervals on each sampling date, using a Flett thermistor.

Statistical Methods

Differences among treatments in the density of each zooplankton species were assessed using two-way ANOVA with repeated measures (Winer 1971; Vanni 1986). This design tested for the main effects of *Chaoborus* and *D. catawba* on the density of resident species, as well as on their interaction. The experiment was divided into two periods (July–August and September–October) and ANOVAs conducted separately for each resident species in each of the two periods, for three reasons.

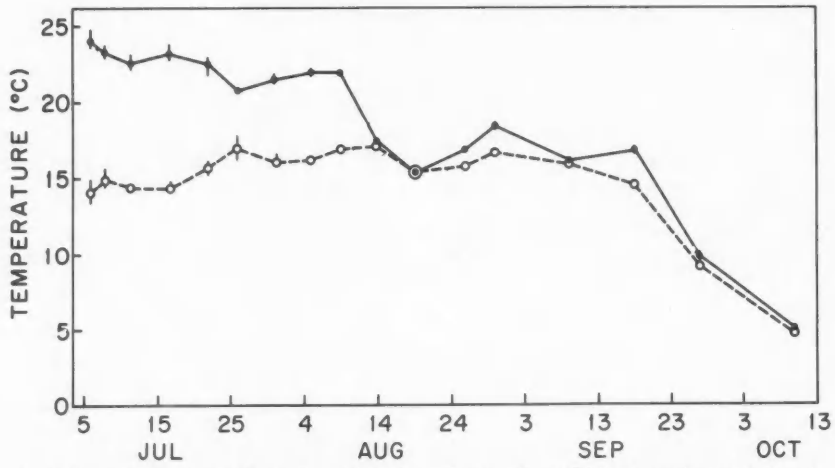

FIG. 1. Mean temperature at the surface (●) and near bottom (3 m) (○) in the enclosures during the experiment. Vertical bars refer to the range of temperatures observed in all 10 enclosures.

Firstly, sampling intervals were longer in September–October than in July–August. Secondly, the density of *D. catawba* was significantly greater in September–October than in July–August. Thirdly, in July–August, *Chaoborus* populations were dominated by instar II and III individuals, while in September–October, *Chaoborus* populations were dominated by instar IV individuals. Thus, the "treatment effects" of *D. catawba* and *Chaoborus* were probably different in July–August than in September–October. There were 10 postmanipulation sampling dates in the first time period and four in the second. All zooplankton density data were log-transformed before ANOVA to stabilize variance. ANOVAs were done using the SAS GLM procedure. For some species, the *D. catawba* × *C. americanus* interaction was significant. If so, I compared particular treatment means with a *t*-test

Demographic parameters (b and d) were analyzed with ANOVA (without repeated measures design). To do so, "critical periods" during which densities between treatments diverged were identified. For each enclosure, a b (d) estimate was obtained for each interval, and a mean b (d) was obtained by averaging the b (d) values from each enclosure within the critical period. Thus a single value b (d) was obtained from each enclosure. Differences in these values among treatments were then tested with ANOVA; thus, $n = 2$ or 3, depending on the number of enclosures in the treatment.

To assess the similarity of initial conditions in the enclosures, the initial densities of the five most common crustaceans and the most abundant rotifer species were compared using two-way ANOVA. For each of these six species, a mean was calculated for each enclosure from the two premanipulation sampling dates and analyzed as with the demographic data.

To compare community structure among treatments, a similarity index (Sale 1984) was calculated for each pair of treatments on five dates, including one premanipulation date (the five dates are those on which measurements of zooplankton were made). Similarity was measured as

$$C_{ij} = 1 - 0.5 \sum_{k=1}^{s} |p_{ik} - p_{jk}|$$

where C_{ij} is the proportion similarity between treatments i and j and varies from 0 to 1, and p_{ik} and p_{jk} are the proportions of total zooplankton community biomass composed of the kth species in the ith and jth treatments. Within-treatment (among replicate enclosures) similarities were also calculated on the final date (10 October).

Results

Thermal and Initial Conditions

Initial densities of each of the six zooplankton species examined, *D. galeata mendotae*, *B. longirostris*, *Diaphanosoma birgei*, *Diaptomus* spp., *Mesocyclops edax*, and *Keratella cochlearis*, were not significantly different among treatments ($P > 0.05$).

During the first month of the experiment, enclosure surface temperature was >20°C and enclosures were thermally stratified (Fig. 1). After this time, temperature declined and enclosures were isothermal. Depth-specific temperatures of enclosures were always within 1° of each other and the lake.

Dynamics of Introduced Species

Both *Chaoborus* and *D. catawba* successfully colonized the Lake 221 enclosures (Fig. 2). *Chaoborus* declined substantially within the first 10 d after introduction and then maintained relatively constant within-treatment densities thereafter (Fig. 2). *Chaoborus* was significantly more abundant in the +*Chaoborus* and *D. catawba* treatment than in the +*Chaoborus* treatment ($P < 0.01$; Table 2). However, the difference was probably not due to any nourishment provided by the addition of *D. catawba* because the divergence in *Chaoborus* density occurred before *D. catawba* was introduced (Fig. 2). The *Chaoborus* populations were dominated by instar II and III individuals at the beginning of the experiment, instar III individuals in August, and instar IV individuals in September and October (Fig. 2).

Daphnia catawba increased exponentially in both the +*D. catawba* and +*Chaoborus* and *D. catawba* treatments until early September, after which *D. catawba* densities remained relatively constant in enclosures without *Chaoborus* and declined in enclosures with *Chaoborus* (Fig. 2). *Daphnia catawba* densities were not significantly different between

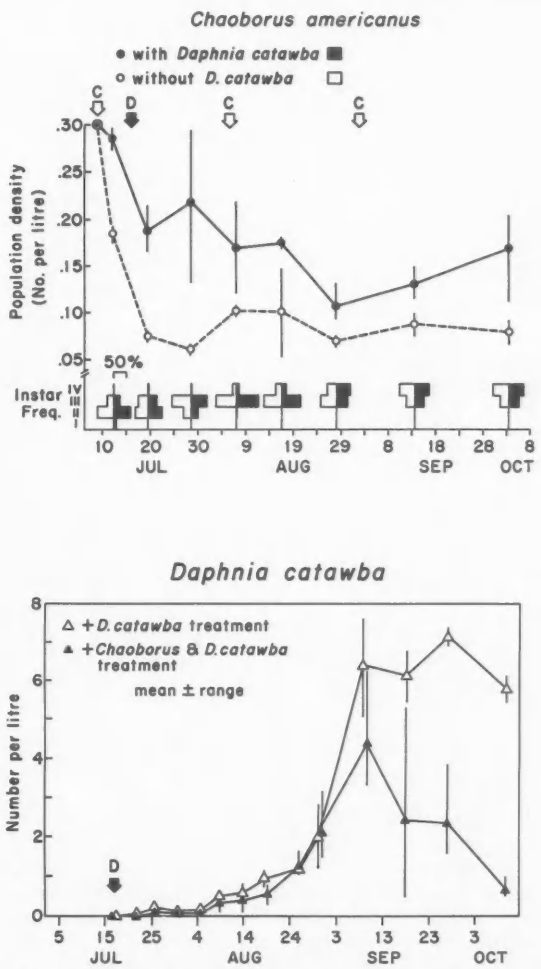

FIG. 2. Dynamics of the introduced species in the enclosures. Top panel: mean (± range) density and instar frequency of *C. americanus*. *Chaoborus* densities represent an average of two biweekly samples. Arrows with "C" denote the time of initial and subsequent *Chaoborus* introductions, and arrow with "D" denotes time of *D. catawba* introduction. Bars at bottom denote frequency of four larval instars in the enclosures. Bottom panel: mean (± range) density of *D. catawba* in the enclosures. Arrow as in top panel.

treatments in July–August ($P > 0.35$) or in the September–October period as a whole ($P = 0.105$). However, considering only the final three dates (18 September – 10 October), densities of *D. catawba* were significantly lower in the presence of *Chaoborus* ($P < 0.05$). From 30 August to 10 October (four sampling intervals), mortality rates of *D. catawba* (*d*) were significantly higher in enclosures with *Chaoborus* than in enclosures lacking *Chaoborus* ($P < 0.05$; Fig. 3). Birth rates were not significantly different between treatments during this time ($P > 0.25$; Fig. 3), suggesting that the decline of *D. catawba* was due to predation by *Chaoborus*.

Dynamics of Resident Species in Response to Introduced Species

Six taxa exhibited reduced density in the presence of *Chaoborus* in at least one of the periods; two species were consistently reduced in density in the presence of *D. catawba* (Table 2).

Daphnia galeata mendotae was reduced to virtual extinction by *Chaoborus* (Fig. 4). The effect of *Chaoborus* on *D. galeata mendotae* was highly significant ($P < 0.001$) in both periods (Table 2). I defined the "critical period" for demographic analysis, during which *D. galeata mendotae* declined in response to *Chaoborus*, as 12–26 July (after 26 July, *D. galeata mendotae* was too rare for demographic analysis in enclosures with *Chaoborus*). During this critical period (three sampling intervals), *D. galeata mendotae* mortality rates were approximately three times higher in treatments with *Chaoborus* than in treatments without *Chaoborus* ($P < 0.005$; Fig. 5). Birth rates were unaffected by *Chaoborus* during this period ($P > 0.05$; Fig. 5).

Daphnia galeata mendotae was not affected by *D. catawba* during July–August ($P > 0.45$), but exhibited significantly lower densities in the +*D. catawba* treatment than in the Control treatment in September–October ($P < 0.001$; Fig 4; Table 2). During the period of 30 August–10 October, *D. galeata mendotae* mortality rates were significantly higher in the +*D. catawba* treatment than in the Control ($P < 0.005$), while birth rates were not significantly different between treatments ($P > 0.25$; Fig. 5). During this time, total phytoplankton abundance tended to be lower in the +*D. catawba* treatment relative to the Control (Table 3). However, the difference is not significant ($P > 0.10$). Comparison of the eight most common algal species (which together comprised ~75% of total phytoplankton biomass), as well as the abundance of major groups of phytoplankton, failed to reveal any significant differences between the two treatments ($P > 0.10$ in all cases).

Bosmina longirostris was reduced in abundance in enclosures containing either *Chaoborus* or *D. catawba* in July–August ($P < 0.05$; Table 2). Between 17 July and 14 August, *Bosmina* mortality rate tended to be higher in the two treatments with *Chaoborus* (Fig. 5); however, the effect of *Chaoborus* was only marginally significant ($0.05 < P < 0.10$). *Daphnia catawba* had no significant effects on *Bosmina b* or *d* ($P > 0.10$ in both cases); however, there was a significant *D. catawba* × *Chaoborus* interaction on birth rates ($P < 0.05$), and it appears that *Bosmina b* was reduced by *D. catawba* in the absence of *Chaoborus* but not in the presence of *Chaoborus* (Fig. 5). During the time *Bosmina* was significantly less abundant in the *D. catawba* treatment compared with the Control (essentially all dates after *D. catawba* introductions), there were no significant differences in total phytoplankton abundance or any of the phytoplankton groups/taxa ($P > 0.05$; Table 3).

Bosmina recovered partially in the +*Chaoborus* treatment in September–October (Fig. 4). The effect of *Chaoborus* on *Bosmina* density was not significant ($P > 0.25$) during this time, while the effect of *D. catawba* was again significant ($P < 0.05$).

Diaphanosoma birgei was unaffected by either introduced species in July–August ($P > 0.50$ in both cases), but was significantly reduced in abundance in the presence of *Chaoborus* in September–October (Table 2; Fig. 4). While the main effect of *D. catawba* was not significant in September–October, there was a significant *D. catawba* × *Chaoborus* interaction (Table 2). Results of *t*-tests revealed that *D. catawba* reduced *Diaphanosoma* density in the absence of *Chaoborus* ($P = 0.06$), but not in the presence of *Chaoborus* ($P = 0.97$). *Diaphanosoma* was too rare in the enclosures to conduct demographic analysis.

TABLE 2. Results of ANOVAs testing for the effects of *C. americanus* and *D. catawba* on densities of zooplankton in the experiment. $*P < 0.05$; $**P < 0.01$, $***P < 0.001$; ns = not significant ($P > 0.05$); — = species was not present in sufficient numbers to conduct ANOVA. ↑ = species was significantly increased in abundance by the introduced species; all other species were significantly decreased.

	July–August			September–October		
Resident species	*Chaoborus* effect	*D. catawba* effect	D × C int.	*Chaoborus* effect	*D. catawba* effect	D × C int.
Cladocerans						
Daphnia galeata mendotae	***	ns	ns	***	***	***
Bosmina longirostris	*	*	*	ns	*	ns
Diaphanosoma birgei	ns	ns	ns	***	ns	*
Holopedium gibberum	ns	ns	ns	—	—	—
Copepods						
Diaptomus spp.	*	ns	ns	***	ns	*
Mesocyclops edax	↑*	ns	ns	ns	ns	ns
Tropocyclops prasinus	ns	ns	ns	ns	ns	ns
Nauplii	**	ns	ns	ns	ns	ns
Rotifers						
Conochilus unicornis	**	ns	*	—	—	—
Keratella cochlearis	ns	ns	ns	—	—	—
Kellicottia spp.	ns	ns	ns	—	—	—
Polyarthra vulgaris	ns	ns	*	ns	ns	*
Trichocerca cylindrica	ns	ns	ns	—	—	—
Introduced species						
Chaoborus americanus	—	**	—	—	**	—
Daphnia catawba	ns	—	—	ns	—	—

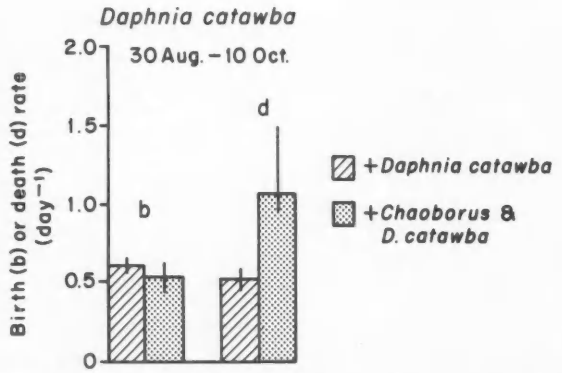

FIG. 3. Mean (±range) per capita instantaneous birth and death rates of *D. catawba* in the enclosures during 30 August–10 October.

Diaptomus was reduced significantly in density by *Chaoborus* (Table 2; Fig. 6), especially in September–October (Fig. 6). Separate enumeration of the two *Diaptomus* species on 27 September revealed that both *D. minutus* ($P < 0.01$) and *D. oregonensis* ($P < 0.001$) were significantly reduced in abundance by *Chaoborus*. Although the main effect of *D. catawba* on *Diaptomus* was not significant in either period ($P > 0.10$; Table 2), there was a significant *D. catawba* × *Chaoborus* interaction in September–October. Results of *t*-tests revealed that in the presence of *Chaoborus*, *Diaptomus* density was lower in the presence of *D. catawba* ($P = 0.005$), while in the absence of *Chaoborus*, *Diaptomus* density was actually higher in the presence of *D. catawba* ($P = 0.10$).

Three other resident Lake 221 taxa were affected by *Chaoborus* during July–August. The cyclopoid copepod *M. edax* was significantly more abundant in the presence of *Chaoborus* in July–August, although *Mesocyclops* eventually declined in all treatments (Fig. 6; Table 2). Copepod nauplii (cyclopoids and calanoids combined) and the colonial rotifer *Concochilus unicornis* were both reduced in abundance in the presence of *Chaoborus* in July–August but not in September–October (Table 2); both taxa declined to very low levels in all treatments toward the end of the experiment. While the main effect of *D. catawba* on *Conochilus* was not significant, there was a significant *D. catawba* × *Chaoborus* interaction in July–August (Table 2). *Daphnia catawba* reduced *Conochilus* density in the absence of *Chaoborus* ($P = 0.04$, *t*-test), but not in the presence of *Chaoborus* ($P = 0.42$).

The other species in the Lake 221 community were not affected by the treatments (Table 2). The cyclopoid copepod *Tropocyclops prasinus* and the rotifer *K. cochlearis* declined to low levels in all treatments throughout the experiment (Fig. 4 and 6), as did the rotifers *Kellicottia* and *Trichocerca* and the cladoceran *H. gibberum* (Table 2; these species not presented in Fig. 4). *Polyarthra* densities were quite variable in the enclosures, but were not affected by the treatments (Fig. 4).

Similarity indices comparing the resident communities summarize the net effects of *Chaoborus* and *D. catawba* on the Lake 221 community (Fig. 7). Proportion similarity between the Control and +*Chaoborus* treatments and between the +*D. catawba* and +*D. catawba* and *Chaoborus* treatments declined steadily throughout the experiment (Fig. 7), indicating that *Chaoborus* caused the community to greatly diverge from its natural state both in the presence and absence of *D. catawba*. In contrast, proportion similarity between the Control and +*D. catawba* treatments and between the +*Chaoborus* and +*D. catawba* and *Chaoborus* treatments remained high throughout the experiment (Fig. 7), revealing that *D. catawba* had much

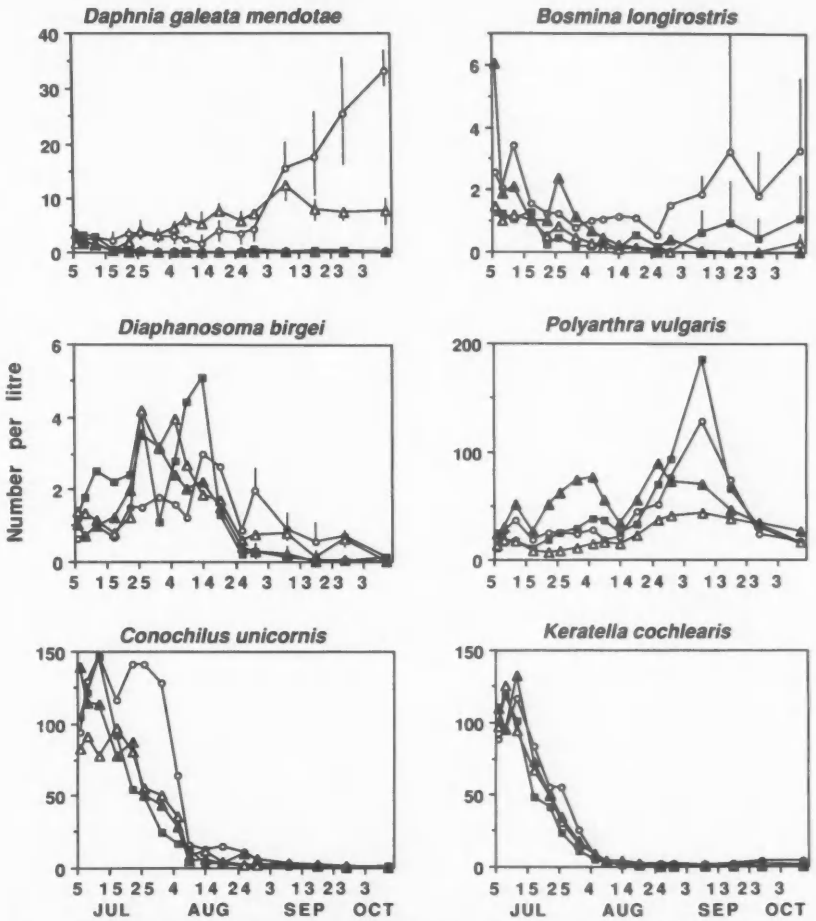

FIG. 4. Mean densities of resident cladocerans and rotifers in the enclosures. Vertical bars denote range or 1 SD and are omitted when treatment means were similar. Arrows denote initial *Chaoborus* (C) and *Daphnia catawba* (D) introductions. ○, Control; △, +*D. catawba*; ■, +*Chaoborus*; ▲, +*D. catawba* and *Chaoborus*.

less of an effect than *Chaoborus* on community structure. Proportion similarity between the Control and the +*D. catawba* and *Chaoborus* treatments and between the +*D. catawba* and the +*Chaoborus* treatments declined throughout the experiment (Fig. 7), again reflecting the strong effect of *Chaoborus*. The mean within-treatment (among replicate enclosures) proportion similarity at the end of the experiment (10 October), when treatment effects were strongest, was 0.863, indicating low variability in community structure among treatment replicates. Furthermore, the initial between-treatment proportion similarities were high (≥0.8, Fig. 7), indicating high uniformity of initial conditions among treatments.

The strong effects of *Chaoborus* on resident Lake 221 zooplankton are also reflected in the differences in mean zooplankton size among treatments (Table 4). Mean mass of the zooplankton communities in the *Chaoborus*-free enclosures increased an order of magnitude during the experiment, reflecting the increase of *D. galeata mendotae*, while mean mass in enclosures without *Chaoborus* remained fairly constant (Table 4). The presence of *D. catawba* had much less effect (Table 4). Because invertebrate predators generally are associated with large mean zooplankton size, these patterns may seem contrary to expected results. However, this can be explained in two parts. Firstly, the mean size calculations do not include the introduced species, which are larger than the resident Lake 221 species. In fishless lakes, mean size is high both because of the presence of these large species and because they reduce the abundance of smaller species. Secondly, all the resident Lake 221 zooplankton species are "small" species; i.e. all are vulnerable to *C. americanus* predation. Within the resident zooplankton community, *Chaoborus* apparently preys most heavily on the crustaceans, leaving the much smaller rotifers to dominate. The net result is a decrease in mean size of resident species. Mean zooplankton mass in the *Chaoborus*-free enclosures also exceeded that of the lake, reflecting the ability of fish (present in the lake) to hold zooplankton size at low levels (Table 4).

Analysis of the crops of *Chaoborus* individuals recovered on 20 October revealed that *Chaoborus* preyed heavily on *D. galeata mendotae* and to a lesser extent on *D. catawba* (Table 5). *Diaptomus*, cyclopoid copepods, and *Keratella* were also

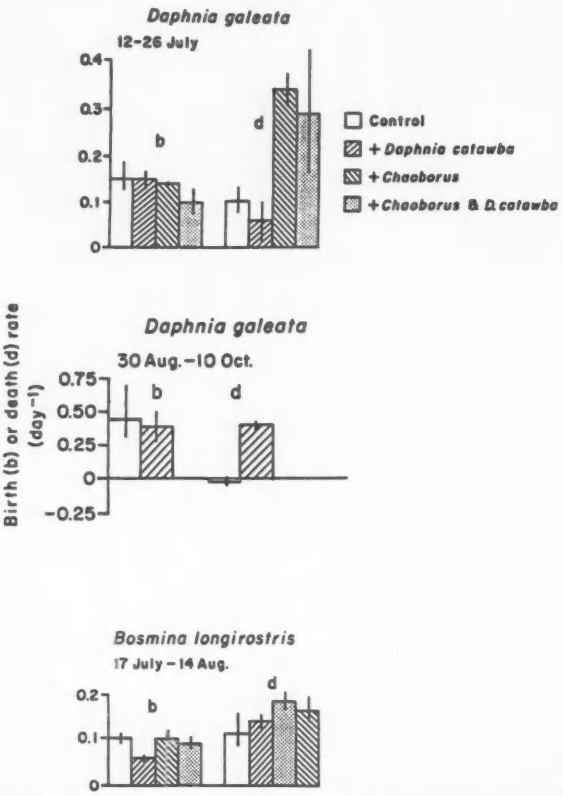

FIG. 5. Mean (± range) per capita instantaneous birth and death rates of *D. galeata mendotae* and *B. longirostris* in the enclosures during specified time intervals.

found in the *Chaoborus* crops (Table 5). Although sample sizes were small, the data indicate that *Chaoborus* preyed on several resident Lake 221 species, as well as *D. catawba*, in the enclosures.

Discussion

This experiment suggests that both invertebrate predation and competition with large herbivores contribute to the scarcity of small species in fishless habitats. Under the conditions of this experiment, *Chaoborus* had more of an effect than *D. catawba* on Lake 221 community structure, as indicated by the similarity indices (Fig. 7) and by species-specific effects (Fig. 4 and 6).

The greater impact of invertebrate predation, compared with competition, found in this experiment agrees with previous conceptual models that depict invertebrate predation as an important determinant of zooplankton community structure (Dodson 1974; Zaret 1980). However, it is possible that competition would be relatively more important under other conditions. For example, if in an experiment of the type described here, the difference between the "large" introduced herbivore and the "small" resident species was greater than that between *D. catawba* and the resident Lake 221 species, the invading herbivore may have depressed food resources to a greater extent and subsequently reduced the abundance of resident zooplankton a greater amount. Thus, for example, in an experiment in which a very large cladoceran, e.g. *D. pulex*, was introduced into a community dominated by very small species, e.g. *Bosmina*, competition may have been more intense (Vanni 1986) and had as much of an impact as invertebrate predation.

The strong effects of *Chaoborus* compared with *D. catawba* in this experiment agree somewhat with the distribution of zooplankton in ELA lakes, although analysis is difficult because data on fishless ELA lakes are scarce. Lake 304, the source of the *Chaoborus* in the experiment, contained large copepods but no cladocerans during 1985 (M. Vanni, unpubl. data), suggesting that *Chaoborus* at high densities can exclude cladocerans. Lake 225, the source of the introduced *D. catawba*, contained two other cladocerans, *B. longirostris* and *H. gibberum*, indicating that these two species can coexist with *D. catawba* at least under certain conditions. Other fishless lakes, which contained *C. americanus* and a relatively large *Daphnia* species, did contain smaller cladocerans, however (Patalas 1971), indicating that these small species can coexist, albeit at low numbers, with large *Chaoborus*.

It is difficult to equate the processes of competition and predation; therefore, care must be taken in comparing the effects of *Chaoborus* and *D. catawba*. In this experiment, for example,

TABLE 3. Mean biomass (mg/m³) of phytoplankton in the Control and +*D. catawba* treatments for all dates after *D. catawba* introduction and during September–October.

	All dates		September–October	
Phytoplankton group/taxa	Control	+*D. catawba*	Control	+*D. catawba*
Total phytoplankton	890	860	999	832
Green algae	254	303	66	27
Botryoccus Braunii	205	256	36	15
Chrysophytes	453	416	690	699
Uroglena americana	126	114	264	251
Dinobryon sertularia	85	91	78	124
Mallomonas akrokomos	62	61	166	168
Salpingoeca sp.	58	44	8	17
Small chrysophytes	63	50	42	31
Diatoms	48	24	117	27
Tabellaria fenestrata	33	16	84	16
Cryptomonads	59	44	97	72
Cryptomonas erosa	22	20	36	35
Cyanobacteria	51	67	4	3

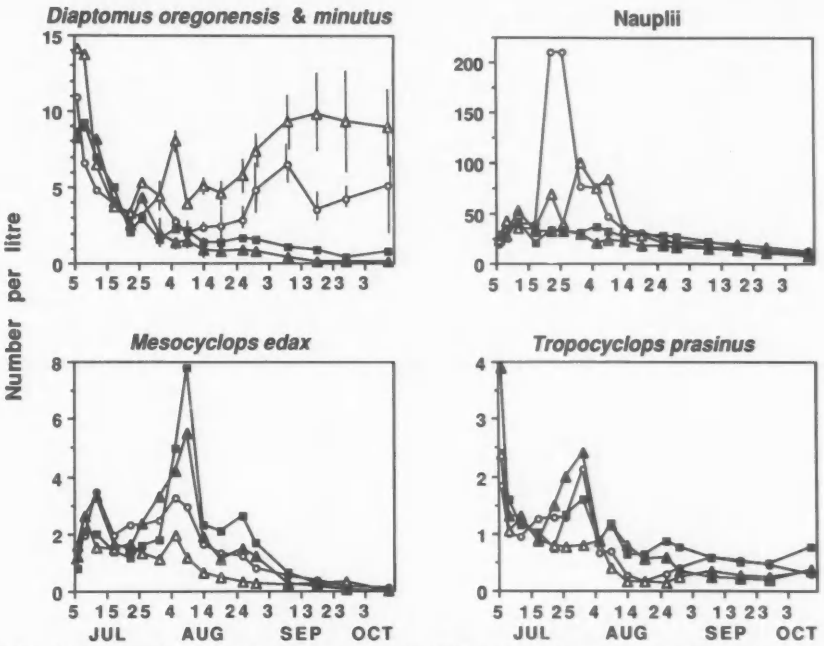

FIG. 6. Mean densities of resident cladocerans and rotifers in the enclosures. Vertical bars denote range or 1 SD and are omitted when treatment means were similar. Arrows denote initial *Chaoborus* (C) and *D. catawba* (D) introductions. ○, Control; △, +*D. catawba*; ■, +*Chaoborus*; ▲, +*D. catawba* and *Chaoborus*.

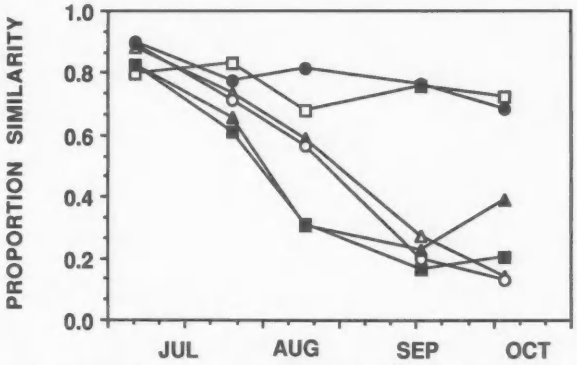

FIG. 7. Proportion similarity of zooplankton communities between treatments on five dates throughout the experiment. 6 July is a pre-manipulation date. □, Control vs. +*D. catawba*; △, Control vs. +*Chaoborus*; ○, Control vs. +*D. catawba* and *Chaoborus*; ▲, +*D. catawba* vs. +*Chaoborus*; ■, +*D. catawba* vs. +*D. catawba* and *Chaoborus*; ●, +*Chaoborus* vs. +*D. catawba* and *Chaoborus*.

due to the nature of the two introduced species and the way in which they were introduced, one may have expected the predator to have larger immediate impacts than the herbivore. Predation involves removal of individuals and thus an immediate effect on population size. In contrast, competition may affect birth rates; therefore the effects of competition may take longer to be expressed. Thus, a potential criticism of the experiment is that it was biased in favor of detecting predation effects relative to competitive effects. However, I feel this is not a serious problem. In analyzing the effects of the introduced species, the experiment was divided into two periods, the second of which assessed the effects of *D. catawba* at highest density (late in the experiment). Even at their highest densities, the effects of *D. catawba* were much smaller than the effects of *Chaoborus* (Fig. 4–7; Table 2). The experiment spanned 3 mo, time for at least seven to eight cladoceran generations. This should be enough time to detect competitive effects expressed through reduced birth rates of resident species.

One potential reason for the apparent weakness of competitive effects of *D. catawba* is that the interactions of resident species obscured any competitive suppression by *D. catawba*. *Daphnia galeata* increased dramatically in the Control treatment (Fig. 4) to densities well above that in the lake. It is possible that the increase in *D. galeata* in the Control treatment affected the smaller cladocerans and rotifers in a manner similar to the way in which *D. catawba* affected smaller species. If so, competitive effects of *D. catawba* would not be detected. The phytoplankton communities in the Control and *D. catawba* treatments were similar (Table 3), suggesting that the two daphnids may have had similar grazing effects and thus similar resource-based competitive effects. However, if both daphnids were in fact depleting resources, phytoplankton should have been much more abundant in the treatments with *Chaoborus* because daphnids were quite rare in these treatments. On the contrary, total phytoplankton abundance in the *Chaoborus* treatment (biomass = 732 mg/m³, all dates after species introductions) and in the *Chaoborus* and *D. catawba* treatment (biomass = 664 mg/m³) was very similar to the treatments lacking *Chaoborus* (Table 3). These differences were not significant, nor were differences in the biomass of common algal species among treatments (M. Vanni, in prep.). This suggests that grazing by *Daphnia* did not control phytoplankton biomass in the

TABLE 4. Mean (± SD) individual zooplankton mass (μg/ind.) in the treatments and in the lake on three dates during the experiment. 6 July is a premanipulation date. All mean mass values exclude the introduced species.

Treatment	6 July	19 August	10 October
Control	0.120 (0.020)	0.308 (0.129)	1.461 (0.168)
+*Daphnia catawba*	0.163 (0.038)	0.589 (0.044)	1.181 (0.503)
+*Chaoborus*	0.107 (0.001)	0.130 (0.005)	0.131 (0.029)
+*D. catawba* and *Chaoborus*	0.124 (0.036)	0.105 (0.022)	0.081 (0.025)
Lake	0.233	0.247	0.992

TABLE 5. Relative abundance of prey items in *Chaoborus* crops and enclosures at the end of the experiment. See Methods for further explanation. *n* refers to the number of crops examined which contained prey items.

Prey taxa	Relative abundance in enclosure	Relative abundance in crops
Control enclosure (n = 10)		
Daphnia galeata mendotae	0.43	0.87
Diaptomus spp.	0.03	0.03
Cyclopoid copepods	0.01	0.10
+*Daphnia catawba* enclosure (n = 7)		
Daphnia galeata mendotae	0.11	0.52
Daphnia catawba	0.13	0.34
Keratella cochlearis	0.004	0.14

enclosures and that resource-based competitive effects of daphnids were weak.

The mechanism by which *D. galeata mendotae* and *Bosmina* were reduced in abundance by *D. catawba* is not clear. As detailed above, *D. catawba* had no detectable effect on phytoplankton biomass (Table 3). It is possible that productivity, rather than biomass, of phytoplankton species, is a more appropriate indicator of food availability to zooplankton; however, this was not measured. It is also possible than some type of chemical interference occurred between *D. catawba* and the resident cladocerans, as has been observed among other zooplankton (Folt and Goldman 1981; Wong et al. 1986). However, it seems unlikely that *D. catawba* could exert chemical interference even at its maximum enclosure density (7.0/L).

In this experiment, the Lake 221 resident *D. galeata mendotae* was affected more than *D. catawba*, the introduced herbivore, by *Chaoborus*. *Daphnia catawba* maintained viable populations, and actually increased in density, in the presence of *Chaoborus* until the *Chaoborus* population was dominated by instar IV individuals (Fig. 2). This is consistent with the observation that *D. galeata mendotae* is rarely found in fishless lakes, in which *C. americanus* is often abundant (Table 1; also Zaret 1980), while *D. catawba* or *D. schoedleri* (a morphologically similar species) is present in fishless ELA lakes (Table 1).

At least two potential reasons can be proposed as to why *D. catawba*, but not *D. galeata mendotae*, is able to coexist with *C. americanus*. Firstly, *D. catawba* attains a larger maximum carapace length than *D. galeata mendotae*; however, there is considerable overlap in carapace length when all individuals in the population are considered (Fig. 8). Size–frequency distributions of entire populations may be misleading, however, because they are dependent on the number of young being produced. When only adult (defined here as egg-bearing) females are considered, a clear trend emerges: *D. catawba* initiates reproduction at a larger size than *D. galeata mendotae* (Fig. 8). By channeling energy obtained in early instars to growth, and attaining a large size at maturity, predation on adult *D. catawba* may be reduced, thereby allowing the population to coexist with *C. americanus* (Lynch 1980). Both Vinyard and Menger (1980) and Spitze (1985) showed that the vulnerability of *D. pulex*, a similar species, to instars III and IV *C. americanus* was highest for individuals ~1.1 mm and declined dramatically for individuals >1.1 mm; individuals >1.4 mm are virtually invulnerable to *C. americanus* predation. The *D. catawba* individuals in the Lake 221 enclosures initiated reproduction at sizes >1.1 mm, while *D. galeata mendotae* initiated reproduction at ~0.9 mm (Fig. 8). Most of the adult female *D. galeata mendotae*, therefore, would be quite vulnerable to *C. americanus* predation, while a large proportion of *D. catawba* adults would be invulnerable.

A second mechanism by which *D. catawba* can reduce predation loss to *C. americanus* is the formation of neck teeth, a crestlike formation along the dorsal margin of the carapace (Krueger and Dodson 1981). Inspection of *D. catawba* individuals in Lake 221 enclosures on 30 August revealed that most (85%, range of replicate enclosures 72–94%) juvenile *D. catawba* in the +*Chaoborus* and *D. catawba* treatment exhibited this antipredation morphology, while it was virtually absent in juveniles in the +*D. catawba* treatment (1%, range 0–2%). Neck teeth are induced chemically by, and reduce predation loss to, *C. americanus* (Krueger and Dodson 1981). The production of neck teeth may have enabled *D. catawba* to coexist with *Chaoborus* in the enclosures. Interestingly, all *D. galeata mendotae* individuals observed from this experiment had well-developed helmets, a device thought to deter some invertebrate predators. Apparently the neck teeth and any associated morphological responses of *D. catawba* are more effective than the helmets of *D. galeata mendotae* in deterring *C. americanus* predation. Havel (1985) found that helmet production did not reduce vulnerability of *D. retrocurva* to *C. americanus* predation. Both *D. galeata mendotae* and *D. retrocurva* do not

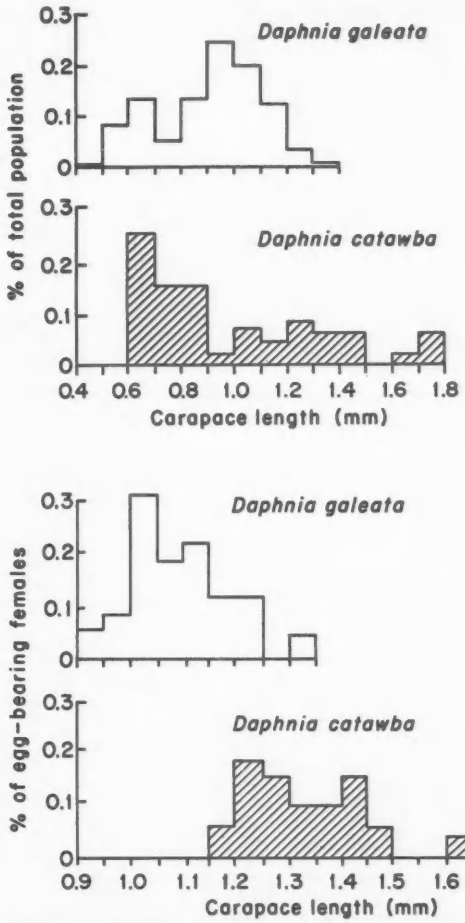

FIG. 8. Size–frequency distributions of *D. galeata mendotae* and *D. catawba* in one enclosure from the +*D. catawba* treatment on 9 September. Top panel: all individuals, $n = 100$ individuals per species. Bottom panel: adult (egg-bearing) females, $n = 50$ individuals per species.

typically coexist with *C. americanus*, and predation by this large *Chaoborus* species probably has not been an important selective pressure on the evolution of helmet morphology in these two daphnids. The helmets, however, may reduce vulnerability to smaller invertebrate predators such as cyclopoids and smaller chaoborids, e.g. *C. punctipennis*, with which *D. galeata mendotae* often coexist.

In summary, this experiment supports previous hypotheses that invertebrate predation may be a very important determinant of freshwater zooplankton community structure. Based on these experiments and the distribution of ELA zooplankton, it is possible to propose some generalizations regarding the mechanisms structuring ELA zooplankton communities. Fishless ELA lakes contain *C. americanus* and sometimes other large chaoborids (Table 1). These lakes do not include the very largest of North American daphnids such as *D. pulex*, perhaps due to some physico-chemical factor, but include *D. catawba* or *D. schoedleri*, which are slightly smaller than *D. pulex*. These species are preyed upon by *Chaoborus* and can be reduced in abundance by fourth instar *C. americanus* (Fig. 2). However, their relatively large size and production of neck teeth allow them a partial refuge from predation by earlier *Chaoborus* instars, and they can coexist with *C. americanus* populations at least during part of the growing season. Smaller zooplankton species are excluded by *C. americanus* predation and to a lesser extent by large daphnids. In lakes with planktivorous fish, fish predation removes the large *Chaoborus* and *D. catawba/schoedleri*, leaving smaller daphnids such as *D. galeata* (Table 1). If planktivorous fish were to be removed from these lakes, we would predict the following sequence of events. First, resident daphnids would increase in abundance and in mean size (Fig. 4; Table 4). Then, larger daphnids and large *Chaoborus* would colonize the lake and reduce the abundance of most resident species. The result would be an increase in mean size of zooplankton, including the new colonists. A potential approach to assessing these predictions would include whole-lake removals of fish, experiments such as those described in this paper, and reciprocal translocations of zooplankton between communities of varying size structure.

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Potential Determinants of Stable Catch in the Brook Trout (*Salvelinus fontinalis*) Sport Fishery in Quebec[1]

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Godbout, L., and R. H. Peters. 1988. Potential determinants of stable catch in the brook trout (*Salvelinus fontinalis*) sport fishery in Quebec. Can. J. Fish. Aquat. Sci. 45: 1771–1778.

Evaluation of four existing empirical models of fish yield showed their applicability to be limited for the brook trout (*Salvelinus fontinalis*) sport fishery in the Laurentian shield because these models explained <60% of the variation in catch. In at least 80% of the lakes, observed catch exceeded that predicted by two of the models. The other models overestimate catch by 100% or more in at least 25% of the lakes. As a first step to improve these models, we identify correlates of "stable catch," defined by the absence of a significant temporal trend in fishing success in lakes for which at least five consecutive years of data were available. Data available or calculable from government sources and maps were used to construct models that identified fish size, lake trophy, altitude, and pH as promising correlates. A second series of models based on our own field determinations confirmed these findings. After fishing effort had been taken into account, these variables reduced the unexplained variation by up to 50%. Although our estimates of trophy and acidity were crude, this study suggests that these indicators should be included in future models to describe and predict the yield of sport fisheries.

L'évaluation de quatre modèles empiriques de rendement du poisson a montré que leur applicabilité était limitée dans le cas de la pêche sportive à l'omble de fontaine (*Salvelinus fontinalis*) dans la région Laurentienne parce que ces modèles expliquaient moins de 60 % de la variation des prises. Dans au moins 80 % des lacs, les prises enregistrées étaient supéreiures à celles prévues par deux des modèles. Avec les autres modèles, la surestimation des prises était de 100 % ou lus dans au moins 25 lacs. Comme première étape en vue d'améliorer ces modèles, nous déterminons des corrélats de « prise stable », définis par l'absence de tendance temporelle importante de la réussite de la pêche dans les lacs pour lesquels nous disposons de données pour au moins cinq années consécutives. Des données accessibles ou calculables à partir de données fournies par le gouvernement et de cartes ont été utilisées pour construire des modèles qui déterminent la taille du poisson, le caractère trophique des lacs, l'altitude et le pH comme des corrélats prometteurs. Une deuxième série de modèles fondés sur nos propres mesures pratiques a confirmé ces résultats. Après avoir tenu compte de l'effort de pêche, ces variables ont réduit jusqu'à 50 % la variation inexpliquée. Même si nos estimations du caractère trophique et de l'acidité étaient rudimentaires, cette étude semble indiquer que ces indicateurs devraient être inclus dans les futurs modèles afin de décrire et de prévoir le rendement des pêches sportives.

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Existing empirical models predict harvest from freshwater fisheries based on morphometric (Rawson 1952; Rounsefell 1946; Hayes 1957), edaphic (Northcote and Larkin 1956), morpho-edaphic (Ryder 1965; Hanson and Leggett 1982), trophic (Hanson and Leggett 1982; Moyle 1956), and biotic variables (Oglesby 1977; Matuszek 1978; Hanson and Leggett 1982; Jones and Hoyer 1982). These models were found to explain from 43 to 84% of the variation in yield of freshwater fisheries.

Unfortunately, several factors limit the applicability of these models to lake sport fisheries. First, existing models rely heavily on commercial catch statistics and are therefore unrepresentative of many recreational fisheries, including those based on natural lakes and fish stocks which dominate the Canadian inland sport fishery. For example, 90% of the lakes in the Quebec brook trout fishery are less than 100 ha in area and less than 10% are stocked (L. Godbout, unpubl. data). In contrast, the models of Ryder (1965), Oglesby (1977), and Matuszek (1978) are restricted to commercial fishing on large lakes (>1000 ha). A third of the lakes used by Hanson and Leggett (1982) were smaller than 100 ha but their fisheries depended on fish stocking programs. Jones and Hoyer (1982) dealt with recreational fisheries, but only two of their 25 water bodies are natural lake and both are larger than 1000 ha. A second problem is that fish yield is poorly defined with respect to the level of exploitation, and consequently, existing models are difficult to evaluate. The Ryder model requires that the lakes be "moderately to heavily exploited," but this is difficult to assess operationally. Other models simply do not define or specify the level of exploitation. Third, existing models are often based on the combined catches of several species, and the proportion of catch constituted by a particular species may vary widely (Paloheimo and Regier 1982). Many sport fisheries are directed at one or

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only a few species of fish. Finally, existing models are likely to produce similar predictions because they are based on relatively small, nearly identical data sets. Over 70% of the lakes used by Ryder (1965) reappear in Oglesby (1977), in one of the models of Hanson and Leggett (1982), and in Matuszek (1978). Consequently, any bias in the data set will affect all models. These difficulties limit the value of existing models of fish yield for the management of single-species, natural sport fisheries, like the brook trout sport fishery of Quebec.

Samson (1973), recognizing these problems, developed a modified version of Ryder's (1965) model for the sport catch of brook trout (*Salvelinus fontinalis*) in Quebec lakes. Vézina (1978) noted that Samson's model explained 60% of the variation in brook trout yield but overestimated the yields of less productive lakes. Vézina produced a model based on mean depth that explained 64% of the variation in fish yield. Both models were based on only a few years of data and a single independent variable. Now that longer series of catch statistics and more complete descriptions of the lakes are available, it is possible to build more comprehensive regressions to identify the potential determinants of catch.

These determinations would be more useful if the new models also incorporated an operational definition of sustainable catch. To this end, we introduce the concept of "stable catch" to indicate the absence of any significant interannual trend in fishing-success (i.e. catch per unit effort of CPUE). Operationally, the catch of a lake is classed as stable if no significant trend ($P \leq 0.05$, Spearman rank correlation) exists between fishing success (number of fish caught per fisherman hour) and year for lakes from which at least five consecutive years of data are available. In practice, more than seven years of data are available for over 95% of the lakes considered here.

This paper first determines the applicability of the models of Ryder (1965), Hanson and Leggett (1982), Samson (1973), and Vézina (1978) to the brook trout sport fishery of Quebec. We were unable to evaluate the models of Oglesby (1977), Matuszek (1978), and Jones and Hoyer (1982) because these require information which is not available for these lakes (primary production, benthos standing stock, and chlorophyll *a* concentration, respectively). Because the four models we tested proved to be biased and imprecise, the second objective of this paper is to offer an improvement on existing models. This is done in two steps. The first identifies the best correlates of stable catch that are available from provincial lake surveys or from topographic and bathymetric maps. Because we had reservations about the quality of these data, the second step evaluates the performance of these variables as correlates of stable catch in an independent data set based on our own site visits to other lakes in the sport fishery. We term these correlated variables "potential determinants" because they are based on correlations involving the data collected in a single visit. Such data may be biased and correlations can be overinterpreted. Nevertheless, this evaluation is an essential step before resources are committed to more intensive study of these lakes or these factors.

Methods

Since the early 1970's, fishing in many of Quebec's wilderness lakes has been closely controlled by the provincial government through a system of parks and reserves. The Ministère du Loisirs, de la Chasse, et de la Pêche of Québec (MLCP) has collected data for fish yield (number per ha, weight per ha) and fishing effort (fisherman-hours) from hundreds of these lakes for up to 15 consecutive years. During this period, access to the lakes was strictly controlled so that fishing pressures were regulated and lay between 1 and 172 fisherman-hours·ha^{-1}·yr^{-1}, depending on the lake. Each day, officers in the reserves and parks assigned the fishing rights to each lake to a set number of fisherman who were selected by lottery. Fishing was permitted from May 15 to September 1 each year and was limited to angling. In most lakes, the fishing boats were also provided by the government and were therefore a standard type. Use of live baitfish was prohibited and no size limits were in force. All fish catches were reported daily to provincial fisheries officers stationed on the access roads or at base camps who weighed and recorded the number and total weight of the fish in the catch. Mean fish size could then be calculated as the total weight divided by the number of fish caught. Fish species composition ws determined using data compiled from minnow traps, gill nets, and fish catch from the MLCP files for each lake.

First, to assess the power of the Ryder (1965), Samson (1973), Vézina (1978), and Hanson and Leggett (1982) models, we used the brook trout yields of 437 lakes, representing all unstocked lakes selected from the MLCP files, because additional information required for the models was available. The concentration of total dissolved solids (milligrams per litre), which is required by the models of Ryder (1965), was determined as $0.67 \cdot \text{Cond}_{25}$, where Cond_{25} is the specific conductance at 25°C (microsiemens per centimetre) (SPOF 1982). Phosphorus concentration, which is the predictor variable in the model of Hanson and Leggett (1982), had been measured for two thirds of the lakes. For the remainder, it was estimated from the loading model of Dillon and Rigler (1975). The loading model requires estimates of drainage basin area, phosphorus export coefficient (assumed to be 4.7 mg·m^{-2}·yr^{-1}; Dillon and Kirchner 1975), and airborne phosphorus input (38 mg·m^{-2}·yr^{-1}; Lachance and Sasseville 1976). Phosphorus retention coefficient was estimated following Ostrofsky (1978), and annual average runoffs were measured in the study area between 1972 and 1976 (0.694 mm·yr^{-1}; Quebec Ministry of Natural Resources). Drainage basin area was determined from topographic maps (1 : 20 000 or 1 : 50 000).

Second, to identify the potential determinants of stable catch, we selected from this global data set of 437 lakes two subsets (series A and B) which met our definition of stable catch. Series A comprised 71 lakes for which estimates were already availbale. Of these 71 lakes, the files of the MLCP indicated that 48 lakes had brook trout as the only fish species ("single-species lakes") and the remaining 23 lakes had additional fish species ("multispecies lakes"). Series B contained 42 lakes which had brook trout as the only fish species. We sampled these lakes once between July 15 and August 20, 1982. The two data sets were intended to be independent. However, because of sampling problems, five lakes are common to both.

Variables of series A (Table 1) were obtained from government standard surveys or were estimated from maps. Shoreline development and mean depth were estimated from bathymetric maps. The mean depth of five lakes for which bathymetric maps were not available was estimated from an empirical relationship for lakes in this region based on lake bathymetric profiles (Bourassa and Joly 1977, MLCP report, Quebec). The slope of the lake basin was estimated as the ratio of maximum depth (metres) to the square root of lake area (square metres). Physico-chemical data were estimated from a single sample col-

TABLE 1. Range of application of the models as indicated by the mean, range, and standard deviation of the regressors for lakes with only brook trout (single-species lakes) and for those with trout and other species (multispecies lakes). All variables, except pH, are transformed to their common (base 10) logarithm. N = the number of lakes.

	Single-species				Multispecies			
	Mean	Range	SD	N	Mean	Range	SD	N
Catch (no.)	2.43	1.25–3.34	0.56	48	2.27	1.18–3.04	0.48	23
Catch weight (kg)	1.51	0.43–2.40	0.52	48	1.28	0.38–2.11	0.46	23
Fishing success (no.·h^{-1})	0.02	−0.47–0.50	0.23	48	−0.06	−0.52–0.58	0.25	23
Fishing success (g·h^{-1})	2.10	1.69–2.62	0.17	48	1.96	1.58–2.58	0.25	23
Fishing pressure (h·ha^{-1})	1.48	−0.08–2.14	0.44	48	1.17	0.10–1.95	0.53	23
Mean weight (g)	2.08	1.67–2.61	0.19	48	2.02	1.65–2.32	0.18	23
Lake area (ha)	0.93	−0.08–1.62	0.40	48	1.15	0.38–2.13	0.50	23
Mean depth (m)	0.51	−0.10–1.11	0.34	35	0.50	0.04–1.10	0.33	20
Maximum depth (m)	0.93	0.18–1.60	0.36	36	0.87	0.30–1.48	0.37	21
Shoreline development	0.20	0.05–0.49	0.11	48	0.22	0.04–0.35	0.08	23
Lake slope (%)	0.45	−0.34–1.04	0.28	36	0.28	−0.28–0.71	0.30	21
Lake altitude (m)	2.63	2.40–2.90	0.11	48	2.64	2.32–2.91	0.15	23
Secchi depth (m)	0.53	0.09–0.81	0.22	16	0.24	−0.22–0.63	0.27	6
Conductivity (μS·cm^{-1})	1.39	1.11–1.72	0.14	35	1.31	1.16–1.45	0.09	13
Total phosphorus (mg·m^{-3})	0.74	0.04–1.08	0.20	48	0.67	0.10–1.07	0.23	23
pH	5.90	4.07–7.38	0.89	22	6.29	5.24–6.76	0.88	3
Drainage basin area (km^2)	0.11	−1.22–1.53	0.49	48	0.53	−0.28–1.75	0.55	23

lected at the deepest point of the lake between July 15 and August 15 (Marsan 1977, MLCP report, Quebec). Lake position within the basin was determined from topographic maps. Total phosphorus was predicted following Dillon and Rigler (1975).

For the second series of lakes (N = 42), we sampled 10–16 lakes in each of three size classes (<20, 40–60, >100–200 ha) between 15 July and 20 August 1982. For each lake, we determined the concentrations of total phosphorus (Menzel and Corwin 1965), total dissolved solids (APHA 1971), chlorophyll *a* (Strickland and Parsons 1971), oxygen (Leeds and Northup Sci. Can.), pH (Fisher model 119), and conductivity (Markson model 101) from an integrated water sample collected between the surface and the thermocline. We also determined reflectance (Bergmann and Peters 1980), Secchi depth, water color (Taylor Water analyzer, Maryland, USA), and turbidity (Hellige Aqua Tester, Thomas Scientific).

Statistical Analysis

Applicability of existing models

To check the applicability of existing models to the brook trout sport fishery, the observed mean catch was regressed against the catch predicted by each model. If a model is accurate in predicting, the coefficient of determination of this regression (R^2) will be unity, and if the model is unbiased, the regression will have a slope of 1 and an intercept of 0. The extent of the departures from this ideal serves as a measure of the predictive power of the model.

Identification of potential determinants

Stable catch was regressed against fishing effort, variance of fishing effort, mean fish size, and lake characteristics to identify the regression which gave the most precise estimate of catch as indicated by high values of R^2 and low values of the mean square error associated with the estimates. The values for catch, effort, and mean fish size used to construct the models are the means of the log-transformed values of all available years for each lake. The importance of fish species composition was evaluated using a dummy variable. This allowed pooling of the data, thus increasing the degrees of freedom of the regression, and hence improving the relative precision of the estimated parameters (Gujarati 1978).

We chose to regress catch as a function of fishing effort because the use of CPUE as the dependent variable assumed that catch was linearly related to effort. This restriction was removed if fishing effort was also used as an independent variable, but this complicated interpretation because it introduced an autocorrelation between the denominator of the dependent variable and one of the predictor variables. We chose not to include fish yield (catch per area) in our analyses for the same reason.

An alternative means of removing the effect of effort is to analyze the residuals of a regression of catch on effort as functions of lake characteristics. This is not appropriate here because effort, (as set by the MLCP) and lake characteristics are not totally independent. Therefore, some of the effects of the determinants of stable catch are removed by regression on effort alone. Thus, the determinants of stable catch cannot be properly identified by regressing the residuals of catch on effort against lake characteristics. Instead, the simplest way to identify potential determinants of stable catch is to regress catch against effort and lake characteristics in a single full model, wherever possible within the limitations set by collinearity.

The best predictors were obtained by a stepwise multiple regression (SAS Institute Inc. 1982). Collinearity between the independent variables was evaluated using the correlation coefficient and the condition index (Belsley et al. 1980). Variables were identified as potentially troublesome if the condition index was greater than 30, and variance-decomposition proportions for two or more estimated regression coefficient variances were greater than 0.5. When collinearity occurred, each collinear variable was used to build separate models that were compared with all other models. The "best" regression models were then identified by the highest values of adjusted R^2 and lowest mean square error. Partial residual regression plots were used to verify that the assumptions of multiple linear regression were satisfied (Larson and McCleary 1972).

TABLE 2. Observed catch (C_w, kg·yr^{-1}) regressed against catch (kg/·yr^{-1}) predicted by the models of Ryder (1965), Hanson and Leggett (1982), Samson (1973), and Vézina (1978). Catch is transformed to their common (base 10) logarithm. Coefficient of determination of (R^2), standard error of the estimate (S_{xy}), and sample size (N) are also listed. Bias is evaluated using χ^2 and the probability (P) indicates the likelihood that there is no bias. *$P < 0.05$. Ryder: [$C_w = 1.4 \cdot (\text{MEI}^{0.45}) \cdot \text{Area}$]; Hanson and Leggett: [$\log C_w = -1.1 + 1.02 \log \text{Phos} + \log \text{Area}$]; Samson: [$\log C_w = 1.02 + 0.17 \log (\text{Cond.}/Z^2) + \log \text{Area}$]; Vézina: [$\log C_w = 0.05 + 0.74 \cdot Z \cdot 0.23 \cdot 0.96^Z + \log \text{Area}$]; Z = mean depth (feet); Area = lake area (ha); Phos = total phosphorus (μg·L^{-1}); Cond. = conductivity (μS·cm^{-1}).

Observed model	R^2	S_{xy}	N	χ^2	P
$\log C_w =$ 0.48* + 0.85* (Ryder)	0.56	0.124	194	64	< 0.0001
1.11* + 0.69* (Hanson and Leggett)	0.53	0.407	209	168	< 0.0001
0.08 + 0.85* (Samson)	0.59	0.341	194	56	< 0.0001
0.06 + 0.90* (Vézina)	0.59	0.358	232	3	$0.05 < P < 0.10$

Results

Applicability of Existing Models

Before generating new models, we used the data from the set of 437 lakes to evaluate the applicability of existing models (Ryder 1965; Samson 1973; Vézina 1978; Hanson and Leggett 1982) to the Laurentian brook trout sport fishery. Not all lakes could be used in each comparison because of missing data, but almost 200 lakes were available to evaluate each of the previous models (Table 2). The coefficients of determination between observed and predicted catch were less than 60%, indicating poor correspondence between observed and predicted catch (Table 2). Existing models are obviously imprecise. They are also consistently biased, since the relationships between observed and predicted catch have a slope significantly less than 1 for all four models. The intercepts were greater than 0 for the regressions involving the models of Ryder (1965) and Hanson and Leggett (1982). This bias was further evaluated using a chi-square test. The null hypothesis that there is an equal number of cases above and below the 1:1 line was rejected in each case except that of the model of Vézina (Table 2).

The models of Ryder (1965) underestimated the observed catch in 80% of the test lakes. That of Hanson and Leggett (1982) underestimated observed catch in 95% of the lakes (Fig. 1). These underestimates were not necessarily small. In half of the lakes, observed catch exceeded the predictions of Ryder's model by at least 50% and the predictions of the model of Hanson and Leggett by at least 85%. Overall the biases in the models of Samson and Vézina were less severe. Nonetheless these models overestimate the catch by at least 100% in a quarter of the lakes (Fig. 1). The catch used in the models of Ryder and Hanson and Leggett were derived from commercial fisheries statistics which were directed to only some of the fish species present. Therefore the differences between the predicted and observed brook trout in catch might be due to the low species richness of the Quebec brook trout lakes, in that all the fish biomass in most of the lakes of this study consists of "target species."

Series A: Data and Models

This first series of models is based on data obtained from government sources for 71 lakes with "stable catches." The domains of application of the models are given by the ranges of the predictor variables for both single and multispecies lakes (Table 1). The major differences between the two types of lakes are that multispecies lakes tend to be larger and have a larger drainage basin and narrower ranges of conductivity and pH. Only variables available for all lakes were used to build the models. The importance of the remaining variables (pH, Secchi depth, conductivity, mean depth, maximum depth) was examined by correlating available data for these variables with the deviations from the full model for the same lakes.

Correlations among the independent variables indicate which variables are so highly related that they might therefore introduce problems of collinearity into the regression model. High correlations (0.7–0.9) were between mean depth, maximum depth, and slope, and these variables ought not be considered simultaneously in regression analysis. In addition, there may be problems associated with collinearity between phosphorus and altitude and among effort, lake area, and variance of effort.

Regression analysis identified five models (Table 3) which were approximately equal in terms of explained variation. These are the best of the 16 models constructed in the sense that they explained most of the variation in catch and had the lowest residual errors; they are also representative in the sense that they are consistent with the effect of morphology and trophy described by other, less powerful models.

These different models have many similarities. The most powerful single predictor of stable catch in all models is fishing effort, explaining 81–83% of the variation in catch (Table 3). Because the slope associated with fishing effort does not differ from unity, CPUE is independent of effort over the range of fishing efforts in this data set. The significance of the dummy variable for species composition indicates that the presence of other species lowers the stable catch of brook trout. Altitude explained an additional 4–5% of the variation in catch (models 1 and 4, Table 3) and showed that catch tends to increase with lake altitude. All "number" models isolated fish size as an important factor that explained an additional 5% of the variation (Table 3) and suggested that lakes with bigger individuals yield smaller numbers of fish.

Although fishing effort, mean fish size, and species composition are the most important and consistently significant correlates of catch, several other variables are significant in at least one regression. Nearly as much of the variation in the number of fish caught can be explained by the combination of total phosphorus concentration and lake area (models 1 and 2, Table 3) as by lake altitude. The concentration of total phosphorus and an interaction term for lake area and species composition also explains a similar amount of variation (model 3, Table 3). This interaction suggests that the trout catch in multispecies lakes is independent of lake area, but greater in larger single-species lakes. As a result, CPUE increases with lake area in single-species lakes.

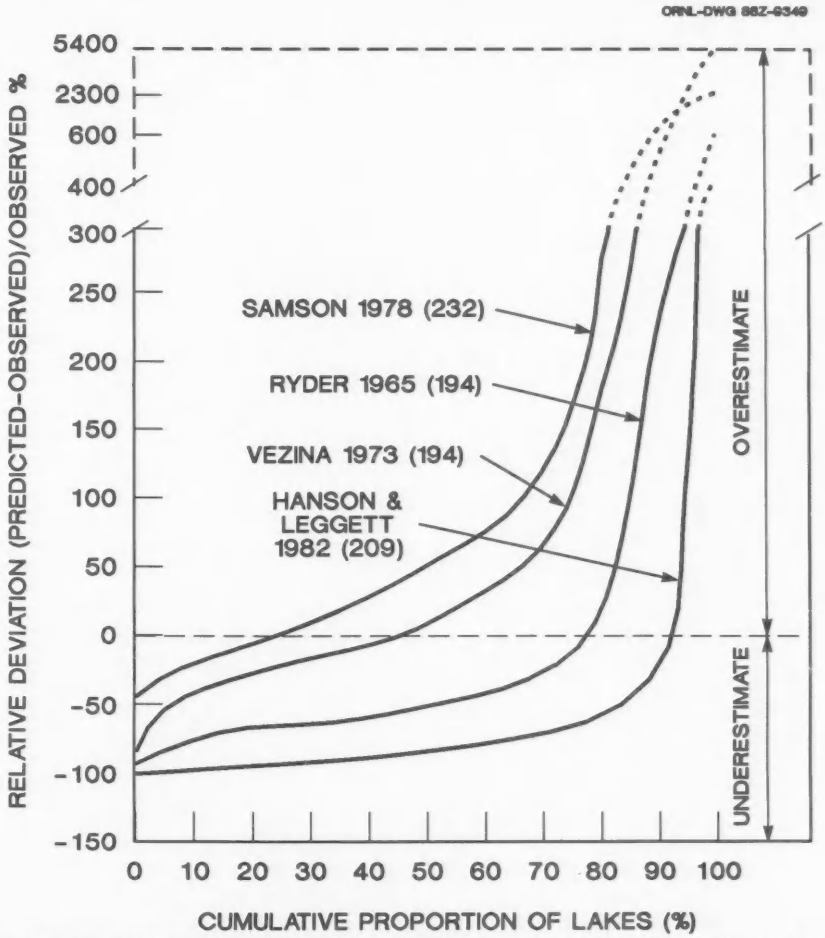

FIG. 1. Cumulative proportion of lakes with deviation less than or equal to indicated value for the models of Samson (1973), Ryder (1965), Vézina (1978), and Hanson and Leggett (1982). The number of lakes used in each comparison is given in parentheses.

Inferences from the mass models are similar to those from the "number" models, except that weight of catch is independent of the individual mean weight. Both number and weight models suggest that catch increases more slowly than area and, consequently, that catch per unit area ("yield") tends to decrease in larger lakes. Correlation of the residuals of these models against other available data showed that pH is positively correlated ($P < 0.05$; $N = 25$) with the residuals of both models 1 and 4, suggesting that acidification reduces stable catch. None of the other variables that were available for only part of the data set (transparency, conductivity, mean and maximum depth) were significantly correlated with the residuals of any of the models in Table 3.

Series B: Data and Models

The lakes sampled to provide the data for the second series of models have greater ranges in area, phosphorus, and conductivity than lakes used for the first series of models. In addition, the ranges of total phosphorous and conductivity for series B lakes are, respectively, 4 and 10 times greater than those observed in the single-species lakes of series A (Table 4). Relationships among variables are similar to those in series A, except that lake area is more strongly related to altitude ($r = -0.54$) and fishing effort ($r = 0.87$). The best models predicting stable catch for series B (Table 5) included fishing effort and the individual mean weight and, with other variables, explained 91–93% of the variation in catch. All models identified an index of trophic status (one of chlorophyll *a*, reflectance, or Secchi depth) which explains 0.3–5% of the variation in catch. Since catch rises approximately as the fourth root of chlorophyll concentration, trout catch rises relatively slowly with lake trohy. This is confirmed by the strongly inverse relation between reflectance, which varies inversely with trophic status, and catch. An additional 1–4% of the variation can be explained by either lake altitude or water color (models 6, 7, 9 and 10, Table 5). In the two models that include lake area (8, 11), fish catch increases more slowly than lake area, indicating that fish catch per unit area (yield) is reduced in larger lakes. Catch is inversely related to variation in fishing effort when this variable is offered instead of its correlate, effort (models 8 and 11, Table 5). This suggests that greater variation in fishing effort among fishing seasons may generate smaller catches. Chloro-

TABLE 3. Best models predicting mean stable catch expressed as mean number (C_n) and mean total weight (C_w, kg) of fish caught per year. Log refers to the common logarithm (base 10). The probability (P) of a greater F, the adjusted R^2, the partial R^2 associated with each variable, standard error of the estimate (S_{xy}), and the standard error of the coefficients (SE) are also listed. Effort = fishing effort (h·season^{-1}); W = mean weight of individuals (g); S: S = 1 single-species and S = 0 multispecies; Alt = altitude (m); Area = lake area (ha); TP = total phosphorus concentration (μg·L^{-1}).

	Model	$P > F$	R^2	S_{xy}	SE
1 log C_n =	−0.65	0.1675	91.5	0.16	0.47
	+0.98 log Effort	0.0001	0.81		0.04
	−0.84 log W	0.0001	0.05		0.11
	+0.06 log Effort·S	0.0014	0.01		0.02
	+0.88 log Alt	0.0001	0.04		0.10
2 log C_n =	+1.51	0.0001	89.4	0.19	0.17
	+0.94 log Effort	0.0001	0.81		0.06
	+0.13 log Area	0.0400	0.01		0.06
	+0.15 S	0.0060	0.01		0.06
	+0.24 log TP	0.0400	0.02		0.05
	−0.86 log W	0.0001	0.05		0.12
					0.13
3 log C_n =	+1.70	0.0001	88.6	0.19	0.17
	+0.96 log Effort	0.0001	0.81		0.05
	+0.29 log TP	0.0100	0.02		0.11
	+0.12 log Area·S	0.0100	0.01		0.05
	−0.83 log W	0.0001	0.05		0.13
4 log C_w =	−3.10	0.0001	90.7	0.16	0.48
	+0.92 log Effort	0.0001	0.83		0.05
	+0.10 log Area	0.0700	0.01		0.05
	+0.07 log Effort·S	0.0006	0.02		0.02
	+0.81 log Alt	0.0001	0.05		0.17
5 log C_w =	−1.21	0.0001	87.9	0.18	0.15
	+0.93 log Effort	0.0001	0.83		0.06
	+0.15 log Area	0.0200	0.01		0.06
	+0.16 S	0.0200	0.01		0.05
	+0.26 log TP	0.0005	0.03		0.11

TABLE 4. Range of application of series B as indicated by the mean, range, and standard deviation of the regressors. All variables, except pH, are transformed to their common logarithms (base 10).

	Mean	Range	SD	N
Catch (no.)	3.32	1.94–4.56	0.62	42
Catch weight (kg)	2.28	0.99–3.57	0.60	42
Fishing success (no.·h^{-1})	0.27	0.28–0.64	0.19	42
Fishing success (g·h^{-1})	2.23	1.85–2.64	0.19	42
Mean weight (g)	1.96	1.59–2.31	0.15	42
Fishing pressure (h·ha^{-1})	1.49	0.95–2.16	0.32	42
Lake area (ha)	1.55	0.32–2.82	0.62	42
Mean depth (m)	0.52	−0.24–1.20	0.38	42
Maximum depth (m)	0.87	0.10–1.66	0.42	38
Altitude (m)	2.83	2.54–2.94	0.11	41
Secchi depth (m)	0.39	0.00–0.85	0.19	42
Conductivity (μS·cm^{-1})	1.35	0.92–2.62	0.33	42
Chlorophyll a (mg·m^{-3})	0.15	−0.40–0.74	0.27	42
Total phosphorus (mg·m^{-3})	1.09	0.66–1.66	0.21	42
pH	6.46	5.27–7.14	0.44	42
Drainage basin area (km^2)	1.09	−1.22–1.53	0.21	42
Water color (platinum)	1.34	0.40–2.10	0.54	40
TDS (mg·m^{-3})	1.87	0.65–2.76	0.42	42
Turbidity (Jackson)	0.56	0.18–0.83	0.15	39
Reflectance (%)	1.81	1.54–1.91	0.08	42

TABLE 5. Best models predicting stable catch expressed in terms of mean number (C_n) and mean weight (C_w). The probability (P) of a greater F, the adjusted R^2, the partial R^2 associated with each variable, standard error of the estimate (S_{xy}), and the standard error of the coefficients (SE) are also listed. Effort = fishing effort (h·yr^{-1}); Vle = variance of fishing effort; W = mean weight of individuals (g); Area = lake area (ha); Chl-chlorophyll a (mg·m^{-3}); Color = water color (platinum); Reflec: reflectance (5); Alt = altitude (m).

Model	$P > F$	R^2	N	S_{xy}	SE
5 log C_n = −1.21	0.0001	96.30	42	0.119	0.52
+0.85 log Effort	0.0001	0.91			0.03
+0.99 log Alt	0.0001	0.04			0.20
+0.26 log Chl	0.0011	0.003			0.07
−0.48 log W	0.0005	0.01			0.13
7 log C_n = −1.27	0.8300	94.5	40	0.142	0.15
+0.91 log Effort	0.0001	0.90			0.04
+0.25 log Chl	0.0097	0.01			0.09
+0.12 log Color	0.0135	0.03			0.05
−0.49 log W	0.0030	0.01			0.15
8 log C_n = +7.39	0.0001	89.1	42	0.205	0.83
+0.78 log Area	0.0001	0.74			0.05
−1.40 log Reflec	0.0030	0.03			0.44
−1.34 log W	0.0001	0.09			0.21
−2.43 Vle	0.0001	0.05			0.46
9 log C_w = −4.23	0.0001	96.0	42	0.119	0.52
+0.85 log Effort	0.0001	0.91			0.03
+1.00 log Alt	0.0001	0.02			0.20
+0.26 log Chl	0.0011	0.01			0.07
+0.52 log W	0.0002	0.02			0.13
10 log C_w = −1.67	0.84	94.6	40	0.143	0.15
+0.91 log Effort	0.0001	0.90			0.04
+0.25 log Chl	0.0095	0.02			0.09
+0.12 log Color	0.0144	0.01			0.05
+0.51 log W	0.002	0.01			0.15
11 log C_w = +3.65	0.0001	87.7	42	0.209	0.84
+0.78 log Area	0.0001	0.80			0.05
−1.38 log Reflec	0.0038	0.05			0.45
−2.31 Vle	0.0001	0.03			0.46

phyll a and pH were collinear and could not be considered together but pH had a significant positive effect on catch if chlorophyll a was excluded from the regression.

Discussion

We chose to construct models using all significant variables to identify the potential determinants of stable catch. One shortcoming of this approach is that the importance of variables other than effort appears negligible. In underexploited lakes, the effect of effort may obscure the effect of other factors; however, the high yields observed relative to expectations based on other models make this unlikely in these lakes. In any case, the importance of the correlates of stable catch is better indicated by the proportion of the variation in catch explained after effort has been taken into account. For example, chlorophyll a and reflectance explain 1–5% of the variation in the full model, but their contribution is not negligible, since this represents 10–50% of the variation after fishing effort has been considered. The importance of these additional variables can be demonstrated by comparing the uncertainties associated with the full model with those of a model based on effort alone. For example, the 95% confidence band in a model based on effort is 1.6 times larger than that estimated from model 9 (Table 5).

Fish size was repeatedly identified as an important correlate of yield. But if fish size is a function of exploitation (Healy 1980), the models may not apply to unexploited systems. However, for these lakes, the relationship between fishing effort and fish size is not significant ($r = -0.14$, $r = 0.09$). This suggests that differences in fish size among lakes reflect different lake characteristics (food quality, disease, accessibility to spawning grounds, etc.) and consequently, fish size adds biotic information not provided by other variables we measured.

This study identified fish size, lake trophic status, lake altitude, and pH as potential determinants of brook trout fish catch. Although crudely estimated, these variables explain an important part of the variation remaining after effort has been taken into account. These variables should be considered whenever more intensive sampling programs are undertaken to provide a basis for the management of natural fish stocks in recreational lakes.

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Inferring the Distribution of the Parameters of the von Bertalanffy Growth Model from Length Moments

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A theoretical approach is described for determining the joint distribution of the parameters of the von Bertalanffy growth model from statistical moments of length. The approach extends the work of K. J. Sainsbury, who had demonstrated that different mean parameter estimates are obtained by assuming that the von Bertalanffy equation applies to individual fish rather than to groups of fish. Sainsbury articulated the goal of studying the joint probability distributions of K and L_∞ in animal populations and developed a maximum likelihood procedure for estimating the parameters of particular distributional forms describing K and L_∞, which were assumed for mathematical convenience to be statistically independent. The primary goal of the present paper is to provide a framework for future research in generalizing Sainsbury's approach by considering (K, L_∞) to be a random vector described by a joint probability density function and by allowing broader classes of distributions to be considered. Minimum cross-entropy (MCE) inversion, an information–theoretic methodology for approximating probability distributions, is shown to be effective in selecting a reasonable and unique joint distribution corresponding to observable length moments. Appealing features of the MCE methodology include the ability to include prior knowledge of uncertain applicability and the capacity of the resulting approximate distribution to represent potential stochastic dependencies between the von Bertalanffy parameters. Several numerical examples, using simulated and historical data, are presented to illustrate how information about the variation and covariation of L_∞ and K can be inferred from a minimal set of length moments. The directions developed in this paper are far from a practical and useful methodology. The MCE inversion procedure is a "method of moments," with no statistical assessment of reliability. Further research is needed to make this promising pdf approximation scheme better suited for real fisheries problems.

Une approche théorique est décrite afin d'établir la distribution à plusieurs variables des paramètres du modèle de croissance de von Bertalanffy à partir de moments statistiques relatifs à la longueur. L'approche pousse plus loin les travaux de K. J. Sainsbury, qui a démontré que l'on peut obtenir différentes estimations moyennes de paramètres en supposant que l'équation de von Bertalanffy s'applique à chacun des poissons plutôt qu'à des groupes de poissons. Sainsbury a formulé le but de l'étude des distributions de probabilité à plusieurs variables des paramètres K et L_∞ chez des populations animales, et a élaboré une méthode du maximum de vraisemblance en vue d'évaluer les paramètres de formes particulières de distribution décrivant K et L_∞, qu'on a supposé statistiquement indépendants pour des raisons de commodité mathématique. Le but principal du présent article est de fournir un cadre de travail pour les futures recherches en généralisant l'approche de Sainsbury en considérant (K, L_∞) comme un vecteur aléatoire décrit par une fonction de densité de probabilité à plusieurs dimensions, et en permettant de tenir compte de classes de distributions plus larges. L'inversion d'entropie croisée minimale (ECM), méthode théorique pour évaluer approximativement des distributions de probabilités, s'est révélée efficace pour choisir une distribution à plusieurs variables raisonnable et particulière correspondant à des moments observables relatifs à la longueur. Les caractéristiques intéressantes de cette méthode comprennent la possibilité d'inclure des données antérieures d'applicabilité incertaine et la capacité de la distribution approximative résultante de représenter des dépendances stochastiques potentielles entre les paramètres de l'équation de von Bertalanffy. Plusieurs exemples numériques, faisant appel à des données simulées et antérieures, sont présentés afin de montrer comment il est possible d'inférer des données sur la variation et la covariation de L_∞ et de K à partir d'un ensemble minimal de moments relatifs à la longueur. Les orientations élaborées dans cet article sont loin de constituer une méthode utile et pratique. L'inversion ECM est une « méthode des moments » sans évaluation statistique de la fiabilité. Il faut effectuer d'autres recherches pour que cette méthode d'approximation de la fonction de distribution des probabilités convienne mieux aux vrais problèmes des pêches.

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A pervasive problem in quantitative natural resource management is how to infer some property of a complex natural system from indirect, fragmentary, and highly summarized evidence. Although background information is frequently abundant, most available statistical methods either rigidly build it into the analysis or pretend that it is not there. It

is important to develop methods that can merge partial or aggregated information with contextual knowledge of indeterminable relevance into a reasonable picture about some aspect of the state of the fishery. The present paper begins the development of an approach to study the joint probability distribution of the parameters of the von Bertalanffy growth model. While the direction taken, based on asymptotic results from information theory, is far from a complete applied methodology, it explicitly models the available partial evidence while allowing the measured inclusion of prior or background information of unquantifiable validity. Although the focus here will be on inferring information about growth from a limited set of moments of length at several ages, it is hoped that this presentation will stimulate interest in the application of information–theoretic inversion procedures to other difficult inference problems in fisheries.

von Bertalanffy Growth

The von Bertalanffy model is a widely applied mathematical representation of growth in biological entities (von Bertalanffy 1938). While originally developed in the context of theoretical physiology, the model is now understood as a remarkably effective empirical approximation to the growth of individuals of many species and of their component organ systems.

The von Bertalanffy equation

$$(1) \quad l(t) = L_\infty (1 - e^{-K(t-t_0)})$$

describes the tendency of the rate of an animal's growth in length to decrease with age. It is a solution of the simple linear first-order differential equation

$$(2) \quad \frac{dl(t)}{dt} = K(L_\infty - l(t))$$

under the initial condition that

$$(3) \quad l(t_0) = 0.$$

The von Bertalanffy model is determined by three parameters: L_∞, the asymptotic length, K, the Brody growth constant (Brody 1945) (sometimes incorrectly referred to as the growth rate), and t_0, the initial time. The asymptotic length L_∞ is the maximum size the animal can theoretically attain if it is allowed to grow indefinitely. The Brody growth constant K is one of the factors in determining the change of length with time, the other factor being the difference between the current length and the asymptotic length. The initial time t_0 is a parameter controlling the horizontal placement of the von Bertalanffy curve. It can be viewed as an empirical initial condition that needs to be fit, the time at which a fish would have had zero length had it grown along the von Bertalanffy curve for its whole life. Because the von Bertalanffy model often does not fit particularly well near the time origin, most researchers hesitate to invest too much biological interpretation in this quantity. While there is probably no single species that is perfectly described by the von Bertalanffy model, it has been and will probably continue to be an important means by which the growth of biological organisms is summarized and compared (Pitt 1970; Green 1973; Daan 1974; Bowering 1976; Ralph and Maxwell 1977). Many of the alternative growth models in use today can be viewed as embellishments, extensions, or reactions to this venerable representation (Richards 1959; Silliman 1967; Pauly and Gaschutz 1979; Gaschutz et al. 1980; Schnute 1981).

Almost universally, the parameters of the von Bertalanffy equation are estimated in practice from data representing a group made up of many individual animals. Questions have been raised about the efficacy of estimating the von Bertalanffy parameters (Knight 1968; Bayley 1977; Roff 1980) and using them to contrast subpopulations (Gallucci and Quinn 1979). Sainsbury (1980) has shown that there is a crucial difference between assuming that the von Bertalanffy equation applies to individual animals and assuming that it applies to a group of animals.

Sainsbury's Model

Sainsbury (1980) has presented a model in which individual animals are assumed to grow in accordance with the von Bertalanffy growth equation with parameters that are fixed with respect to each fish but which are allowed to vary randomly between fish. This approach was motivated by concerns that a mathematical description of the growth of an individual animal might be inappropriate for describing the typical growth for a population of animals and vice versa. Sainsbury's model for the population essentially becomes the characterization of the probability distribution of K and the probability distribution of L_∞ for the group.

With the assumptions that K and L_∞ are probabilistically independent, that L_∞ is normally distributed, and that K follows a gamma distribution, Sainsbury derived expressions for the expected value and variance of the length at age T, as well as the first two moments of the growth increment I_T. He also presented a maximum likelihood method of estimating the parameters of the assumed probability density functions from collected data.

Focusing on the distinction between $E[e^{-KT}]$ and $e^{-E[K]T}$, Sainsbury demonstrated that different parameter estimates are obtained by assuming that the von Bertalanffy equation applies to individual fish rather than to groups of fish, an observation that should apply to other nonlinear growth models as well.

A sympathetic criticism of Sainbury's model concerns the strong assumptions made about the form of the probability distributions characterizing K and L_∞. As that author pointed out, the selected distributions were chosen as a compromise between reality and analytic tractability. If L_∞ were truly Gaussian, then there is a finite probability of observing a fish with a negative length. While the gamma distribution employed by Sainsbury to describe the variability of K admits a broad class of densities, it also is a function with just a few degrees of freedom, and there are distributional shapes that it fits poorly.

But it is the assumption of probabilistic independence of K and L_∞ that is the most serious limitation of the model. There is considerable evidence that estimates of these parameters significantly covary in natural populations (Knight 1968; Gallucci and Quinn 1979), with empirical assessments of the correlations between K and L_∞ ranging as high as -0.999. Instead of being independent, these parameter estimates are so nearly dependent on each other that it is even possible to consider reparameterizing the growth equation using just one parameter rather than two, an approach initiated by Gallucci and Quinn (1979). It is not clear what inferences about the correlation of the parameters themselves can be made from the strong empirical correlation of the parameter *estimates*, but the possibility of nonindependence merits further study. The primary goal of the present paper is to provide a framework for generalizing Sainsbury's approach by considering (K,L_∞) to be a random

vector described by a joint probability density function and by allowing broader classes of distributions to be considered. Of particular interest will be distributional forms that permit the estimation of the degree of dependence of the two parameters.

An Ill-Posed Inverse Problem

In this paper we explore the possibility of inferring a general joint probability density function $q(L_\infty,K)$ from measured length moments of several age classes. For clarity, we will first assume that the initial time t_0 is known by other means, and we will lose no generality in setting it to zero. Later in the paper, we will relax this assumption and explicitly consider t_0 as a random quantity.

Suppose we have evidence about the distribution of lengths at a succession of ages, in particular, the first two (noncentral) moments. The moments for age class T can be related to the underlying joint density function by means of the integral equations

$$(4)\quad E(l_T) = \iint L_\infty(1-e^{-KT})q^{\text{true}}(L_\infty,K)dL_\infty dK$$

and

$$(5)\quad E(l_T^2) = \iint L_\infty^2(1-e^{-KT})^2 q^{\text{true}}(L_\infty,K)dL_\infty dK.$$

These equations are well-defined from right to left, since if we know the underlying pdf $q^{\text{true}}(L_\infty,K)$, then we can compute expected values unambiguously. Each expected value can be considered an integral constraint on the true pdf, a well-defined mapping of the continuous function of two variables $q^{\text{true}}(L_\infty,K)$ into a single scalar number or moment.

We would like to solve the inverse problem, that is, to deduce a reasonable approximation of $q^{\text{true}}(L_\infty,K)$ given a finite set of first- and second-order moments at several ages. The moments contain diffuse information about the underlying pdf, with the integral kernel acting as a window through which the unknown pdf $q^{\text{true}}(L_\infty,K)$ is indirectly perceived.

This is an example of a class of well-known ill-posed inverse problems with an infinite convex set C of solution pdf's $r(L_\infty,K)$, each consistent with the given set of integral constraints in the form of the measured moments.

Sainsbury turned this ill-posed problem into a well-posed one by assuming a particular form for the solution pdf that has a relatively small number of parameters. Anyone who does this runs the risk of being criticized for choosing a form that does not capture all the qualities of reality that someone else might think important. For example, Sainsbury's model is inadequate for the study of the covariation of L_∞ and K because he assumed that they are independent. In a sense, he has incorporated possibly spurious prior information into the problem in a manner that his estimation technique cannot overcome.

Prior Knowledge

Applied statisticians often express dissatisfaction with formal estimation procedures in statistics because background information has to be either ignored or rigidly adhered to (Hodges and Lehman 1952; Blum and Rosenblatt 1967; Jaynes 1968; Kashyap 1971). Neither position is desirable, nor does it model the processes of human understanding. Contextual knowledge is unquestionably relevant to the applied problem, but difficult to merge gracefully with new information in the form of actual measurements of the system. If we had no new measurements at all, we would base our predictions on our experience with similar systems, or on our experience with the behavior of this particular system in the past. If we had a limited amount of information about the actual system under study, we would want a solution consistent with both the current data and our prior understanding. It would seem reasonable to give precedence to the new accurate knowledge and then resolve any remaining inferential ambiguities by appealing to the prior knowledge base. Kullback's Principle of minimum cross-entropy (Kullback 1959) provides a rule for picking a unique solution using both the new system measurements and the background knowledge. It states that from a set of possible solutions, we should choose the one most similar to our prior information.

Cross-Entropy Minimization

In fisheries management, there is often a wealth of prior information of uncertain applicability about a particular fish stock, coming perhaps from historical records, experience with similar species, or theoretical principles. It would seem reasonable to use Kullback's Principle to resolve the ambiguity of the solution set C by picking the element in C most similar to an assumed prior $p(L_\infty,K)$ that somehow represents our prior understandings. If we have absolutely no insight into the problem area, we would specify a uniform pdf, and our minimum cross-entropy (MCE) procedure would reduce to the well-known maximum entropy (ME) formalism. No matter how the prior density is specified, the selected element must still satisfy all of the given moments because it is chosen from a set composed only of elements that meet all of the moment constraints. Our prior knowledge is never allowed to contradict or restrict the evidence of the current data but guides us to a well-defined solution when the current data is insufficient.

To implement this optimization procedure, it is necessary to be precise about how to measure the dissimilarity between two pdf's $p(L_\infty,K)$ and $q(L_\infty,K)$. In information theory this distance is commonly quantified by Kullback's cross-entropy functional

$$(6)\quad H[q(L_\infty,K),p(L_\infty,K)] = \iint q(L_\infty,K) \times \log \frac{q(L_\infty,K)}{p(L_\infty,K)}\, dL_\infty dK.$$

Also known as the directed divergence, the minimum discrimination information, or the Kullback–Leibler number, this distortion measure on the space of probability density functions can be interpreted as the expected value of a log-likelihood ratio. Cross-entropy has been used previously as a distance measure in fisheries application by several authors (MacDonald and Pitcher 1979; Schnute and Fournier 1980).

Kullback's Principle would have us find the posterior pdf $q(L_\infty,K)$ that minimizes $H[q(L_\infty,K),p(L_\infty,K)]$ while exactly satisfying the set of constraint equations

$$(7)\quad m_j = \iint f_j(L_\infty,K)q(L_\infty,K)dL_\infty dK, \quad j=1,\ldots,M.$$

That is, we are treating m_j as the average value of the scalar kernel function $f_j(L_\infty,K)$ when the true probability density function is $q(L_\infty,K)$. For example, the kernel corresponding to the mean length at age 5 is $f_5(L_\infty,K) = L_\infty(1-e^{-K5})$. It should be noted that the expected value constraints (equations 4 and 5) corresponding to our data are in the form of Eq. 7.

The general problem of pdf approximation using the MCE criterion has been studied, and a solution for the posterior pdf

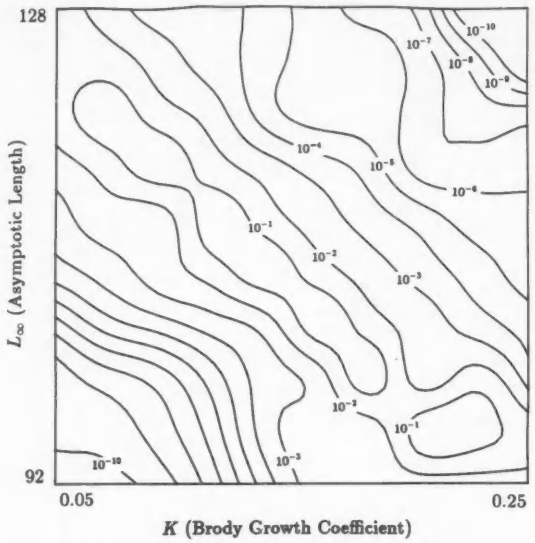

FIG. 1. MCE posterior pdf for Example 1.

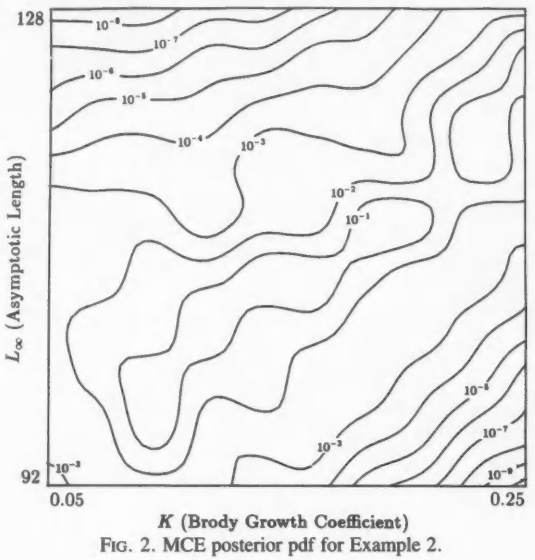

FIG. 2. MCE posterior pdf for Example 2.

$q(L_\infty,K)$ for nonpathological integral kernels $f_j(L_\infty,K)$ is well-known (Shore and Johnson 1981):

$$(8)\quad q^{\text{mce}}(L_\infty,K) = p(L_\infty,K)\exp\{-\sum_{i=0}^{M}\beta_i f_i(L_\infty,K)\}$$

where the $[\beta_i]$ are Lagrange multipliers whose values are made consistent with the measured moments m_j by solving the set of nonlinear equations

$$(9)\quad m_j^{\text{measured}} = \iint f_j(L_\infty,K)p(L_\infty,K)\exp\{-\sum_{i=0}^{M}\beta_i \times f_i(L_\infty,K)\}dL_\infty dK \quad j=1,\ldots,M$$

along with the normalizing constraint

$$(10)\quad 1 = \iint p(L_\infty,K)\exp\{-\sum_{i=0}^{M}\beta_i f_i(L_\infty,K)\}dL_\infty dK.$$

The latter constraint comes about because the posterior $q(L_\infty,K)$ is a probability density function and hence must integrate to unity. In practice we generally have to solve this system of nonlinear equations using numerical methods such as the Newton–Raphson procedures.

A nonrigorous derivation of the form of the MCE posterior density is presented in Appendix B. A detailed consideration of the conditions under which this result exists and is unique, which is beyond the scope of the present paper, can be found in Csiszár (1975) and Johnson (1979). While there are kernel functions f_j for which no unique MCE solution exists, this possibility is rarely relevant in practice. Existence and uniqueness are guaranteed if the kernel functions can be written as a multivariate power series, or if the kernel functions, no matter how discontinuous, are bounded. A review of successful applications of MCE inversion techniques can be found in Shore (1984).

We will now apply this procedure for selecting a unique pdf to the problem of inferring the joint pdf of L_∞ and K from length moments of several age classes, information that is commonly collected, for example, in the determination of age–length keys. Suppose we knew the mean and the mean square of length at three specific ages. We could then write seven equations constraining the true pdf $q^{\text{true}}(L_\infty,K)$:

$$(11)\quad 1 = \iint q^{\text{true}}(L_\infty,K)dL_\infty dK$$

$$(12)\quad m_1 = \iint L_\infty(1-e^{-Kt_1})\,q^{\text{true}}(L_\infty,K)dL_\infty dK$$

$$(13)\quad ms_1 = \iint L_\infty^2(1-e^{-Kt_1})^2 q^{\text{true}}(L_\infty,K)dL_\infty dK$$

$$(14)\quad m_2 = \iint L_\infty(1-e^{-Kt_2})q^{\text{true}}(L_\infty,K)dL_\infty dK$$

$$(15)\quad ms_2 = \iint L_\infty^2(1-e^{-Kt_2})^2 q^{\text{true}}(L_\infty,K)dL_\infty dK$$

$$(16)\quad m_3 = \iint L_\infty(1-e^{-Kt_3})q^{\text{true}}(L_\infty,K)dL_\infty dK$$

$$(17)\quad ms_3 = \iint L_\infty^2(1-e^{-Kt_3})^2 q^{\text{true}}(L_\infty,K)dL_\infty dK.$$

From equation 8 we can directly write the form of the MCE posterior solution:

$$(18)\quad q^{\text{mce}}(L_\infty,K) = p(L_\infty,K)\cdot\exp\{\beta_0 + \beta_1\cdot L_\infty(1-e^{-Kt_1}) + \beta_2\cdot L_\infty^2(1-e^{-Kt_1})^2 + \beta_3\cdot L_\infty(1-e^{-Kt_2}) + \beta_4\cdot L_\infty^2(1-e^{-Kt_2})^2 + \beta_5\cdot L_\infty(1-e^{-Kt_3}) + \beta_6\cdot L_\infty^2(1-e^{-Kt_3})^2\}.$$

The MCE posterior density is completely determined when we fit the Lagrange multipliers β_i to reproduce the measured moments, usually with an iterative numerical procedure. A number of nonlinear minimization techniques seem to work equally well, including Newton–Raphson methods (Gokhale and Kullback 1978), the MINPACK minimization routines (More et al. 1980), and the Nelder–Mead simplex procedure (Nelder and Mead 1965). The following examples with illustrate how effective the MCE procedure is at recovering the latent pdf of the von Bertalanffy parameters.

Example 1

The first two numerical examples, using simulated data, are designed to show how information about the covariation of L_∞ and K can be inferred from a minimal set of length moments. The data, while fictitious, were created to emulate some of the growth characteristics of a slow-growing marine organism like

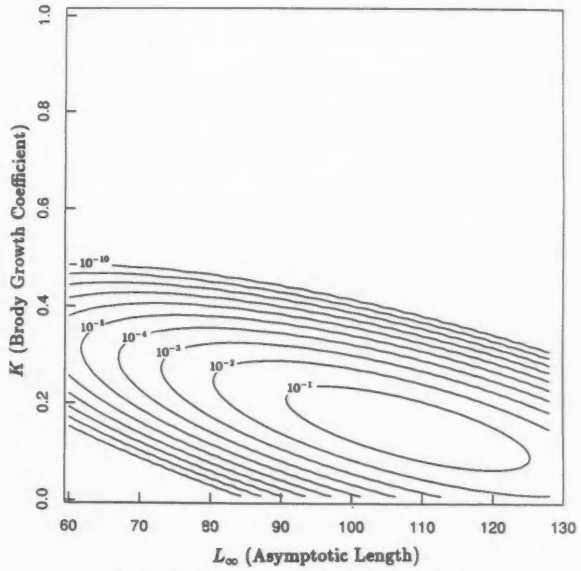

FIG. 3. Simulated true density for Example 3.

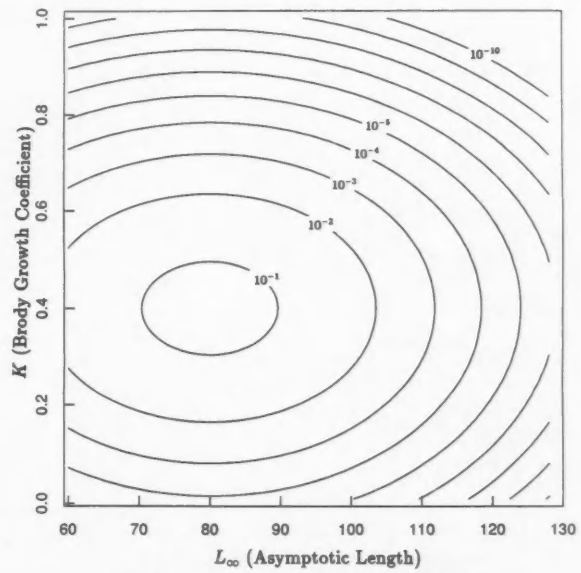

FIG. 4. Assumed prior density for Example 3.

the turbot, which may continue to grow into the second decade of its life. One hundred (L_∞,K) pairs were generated from a bivariate Gaussian distribution such that $\mu_{L_\infty} = 108$ cm, $\sigma_{L_\infty} = 10$ cm, $\mu_k = 0.15$, $\sigma_k = 0.05$, and $\rho_{(L_\infty,K)} = -0.99$. One sample pair thus generated had a K-element less than zero and was discarded. von Bertalanffy curves were computed for each of the remaining pairs and the ensemble mean and mean square "collected" for lengths at ages 1, 10, and 20 yr. While moments at these three ages nicely bracket the initial, intermediate, and asymptotic portions of the growth curves, this example is somewhat artificial in that if we actually collected information at these ages, we would probably also have data about the lengths at all the intermediate ages as well. Nevertheless, this hypothetical example is designed to show that we can deduce a great deal from a very limited set of information. To emphasize the recovery of covariance phenomena, the prior pdf $p(L_\infty,K)$ was assumed to have the same mean and standard deviation in each component as the generating distribution, but to be independent in dimensions, that is $\rho_{L_\infty,K)} = 0.0$.

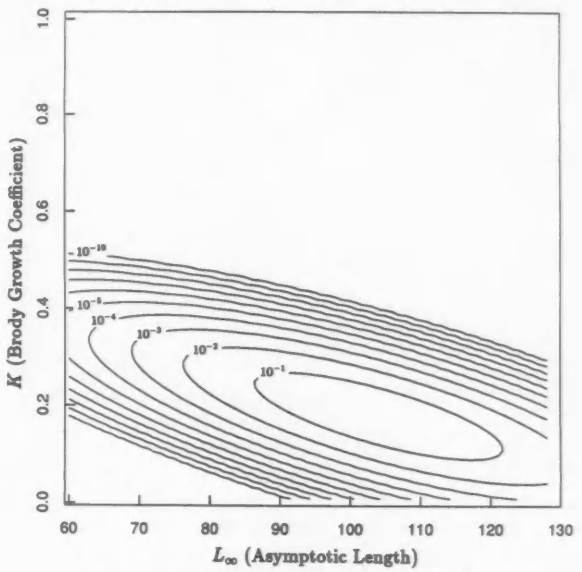

FIG. 5. MCE posterior density for Example 3.

TABLE 1. Porgy data (values inferred by Tanaka (1962) from a length–frequency distribution).

Age	Mean	SD
I	10.99	0.8
II	15.26	1.2
III	19.84	1.4
IV	23.50	1.2
V	26.82	1.4

The Lagrange multipliers $\beta_i, i=0,\ldots,6$, were fit with the Nelder–Mead simplex algorithm to the six estimated moments and the normalizing constraint

$$(19) \quad 1 = \int\int q(L_\infty,K;\{\beta_i\})dL_\infty dK.$$

Figure 1 illustrates the logarithmically spaced equiprobability contours of the MCE posterior pdf for this problem. The information about the interaction of the von Bertalanffy parameters, diffusely encoded in the measured moments, is recovered by the MCE posterior density. It is obvious from inspection of equation 18 that the posterior pdf is not Gaussian, even though the assumed prior density and the true density being approximated are both Gaussian.

Example 2

Another data set was generated, under the same conditions as given in Example 1, except that the correlation between L_∞ and K was set to $\rho = +0.99$. The same independent prior density was assumed as well.

Once again the MCE posterior density for this example, as depicted in Fig. 2, shows the influence of measured length

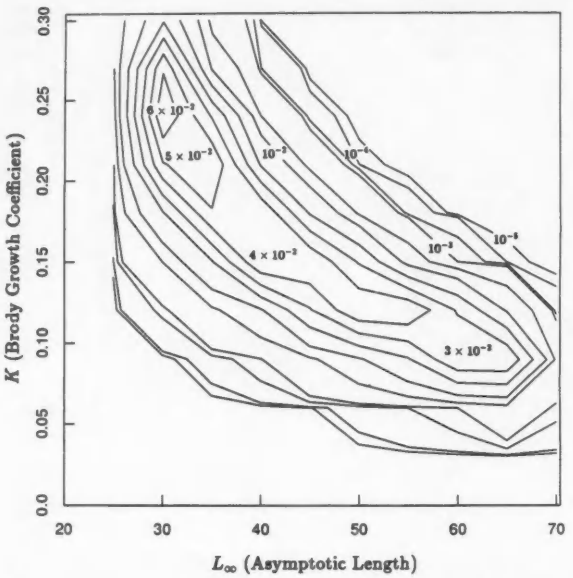

FIG. 6. MCE posterior density for Example 4 (Tanaka's (1962) porgy data).

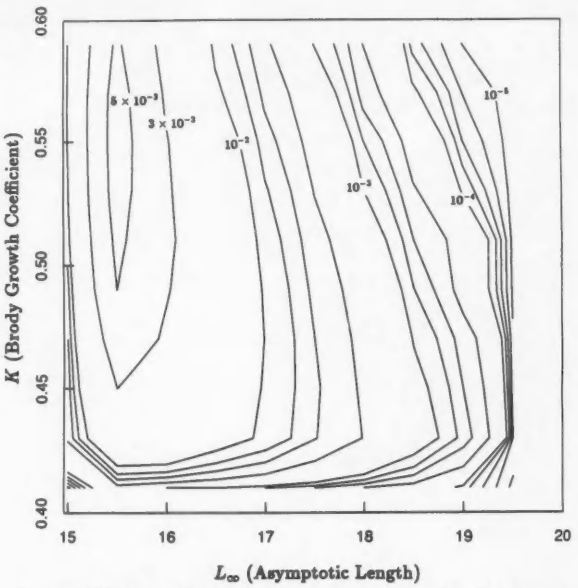

FIG. 7. MCE posterior density for Example 5 (Sund's (1911) sprat data, as reported in Ricker (1969)).

TABLE 2. Sprat data (Sund's (1911) sprat (*Clupea sprattus*) data, as reported by Ricker (1969), composed of back-calculated lengths of the 1903 year-class)

Age	Mean	SD
I	5.86	1.124
II	10.29	1.387
III	12.79	1.056
IV	13.92	0.950
V	14.65	0.868

moments. The interaction of L_∞ and K is strongly apparent in this posterior density.

Example 3

In the preceding examples we have specified a prior pdf with the correct mean and variance in each dimension in order to emphasize the recovery of the covariance information. Example 3 is presented to demonstrate that the MCE procedure can overcome the effects of an unrepresentative prior distribution. One thousand (L_∞,K) pairs were generated from a bivariate Gaussian density, trimmed at zero in both dimensions to preclude negative asymptotic length and negative growth, with parameters $\mu_{L_\infty} = 108$ cm, $\sigma_{L_\infty} = 10$ cm, $\mu_k = 0.15$, and $\rho_{(L_\infty,K)} = -0.70$. A contour plot of this density is depicted in Fig. 3. The prior pdf $p(L_\infty,K)$ was assumed to have parameters $\mu_{L_\infty} = 80$ cm, $\sigma_{L_\infty} = 20$ cm, $\mu_k = 0.4$, $\sigma_k = 0.1$, and $\rho_{(L_\infty,K)} = 0.0$ and is displayed in Fig. 4. Forty moments were "collected" from the simulated data, representing the mean and mean square of length at ages 1–20. A contour plot of the MCE posterior pdf corresponding to this 41-variable nonlinear minimization problem is shown in Fig. 5. Obviously the MCE procedure has recovered the important characteristics of the true density from the length moments, in spite of the choice of prior.

Example 4

Few attempts have been made to apply this MCE method to real fisheries data, in part because generalizable software has not yet been written. Hence, every application currently requires the development of a custom program. Two preliminary analyses will now be presented.

Tanaka (1962) inferred the moments of length-at-age for porgy (*Taius tumifrons*) from a length–frequency distribution collected in 1950. His estimates of the mean and standard deviation for each age are presented in Table 1.

The MCE posterior density, computed using a uniform (noninformative) prior, is presented in Fig. 6, and evidences negative diagonal structure.

Example 5

Ricker (1969) summarized back-calculated length data for a sample of sprats (*Clupea sprattus*) collected in 1908, and analyzed by Sund in 1911. The mean and standard deviation of back-calculated length at various ages for the 1903 year-class are summarized in Table 2.

The MCE posterior density corresponding to these constraints, computed using the uniform prior pdf, is presented in Fig. 7. Negative covariation is less apparent in this example, although there is an interesting slight bulge of probability toward higher L_∞ values for lower K values in this contour plot.

In the preceding discussion we have explicitly assumed that the initial conditions parameter t_0 in the von Bertalanffy model is identically zero, or constant, for all the animals in the group. In many applications, this is not a credible assumption, and we must fit t_0 as well. The general method we have outlined above for two latent variables can be trivially extended to infer a trivariate posterior pdf $q(L_\infty,K,t_0)$ from length moments. In the next section we will consider a special trivariate application that can be reduced to the bivariate formalism just considered.

TABLE 3. Eel data (mark–recapture data for eels (*Anguilla australis*) in the Doyleston Drain, New Zealand, summarized from Fig. 2 in Burnet (1969)).

Mean length at first capture	46.41
SD of length at first capture	12.29
Mean length 1 yr later	50.40
SD of length 1 yr later	11.10
Correlation of length over 1-yr interval	0.9845

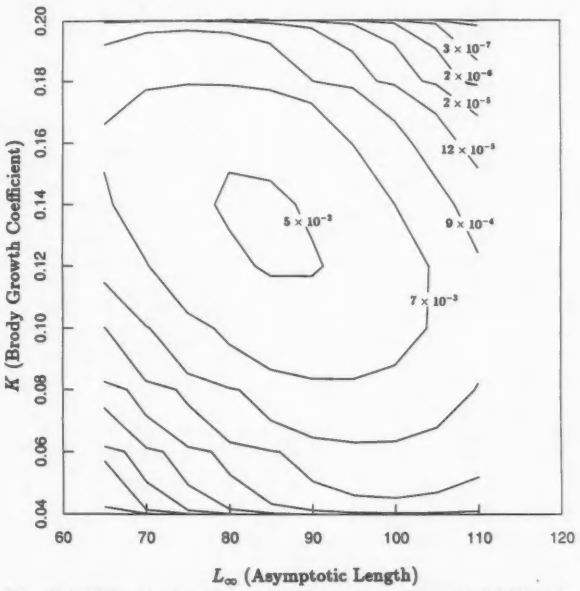

FIG. 8. MCE posterior density for Example 6 (Burnet's (1969) eel data).

Mark–Recapture Experiments

Until this point, the symbol t has really referred to the age of individual animals and not to chronological time. In a population of animals of mixed ages, it is possible to refer to t as actual time by allowing $-t_0$ for each organism to refer to that animal's age at time slice 0. However, to avoid confusion with the entrenched interpretation of t_0, we will introduce a new symbol τ to denote age at time slice 0, $\tau = -t_0$.

In some mark–recapture studies, the age of an animal cannot be determined without sacrificing it, although its length can be determined with an acceptable handling risk. It is of interest to infer the distribution of the von Bertalanffy parameters from the moments of length at two or more specific time points. For example, an investigator might dig up a number of clams of various but unknown ages, measure their lengths, mark each one with a unique identification code, release the animals in their original habitat, and then recapture and remeasure Δ years later.

The mean and mean square of length at each measurement time slice can be expressed as a constraint on the trivariate pdf $q^{\text{true}}(L_\infty,K,\tau)$:

$$(20)\quad E(l_0) = \iiint L_\infty(1-e^{-K\tau})q^{\text{true}}(L_\infty,K,\tau)dL_\infty dK d\tau$$

$$(21)\quad E(l_0^2) = \iiint L_\infty^2(1-e^{-K\tau})^2 q^{\text{true}}(L_\infty,K,\tau)dL_\infty dK d\tau$$

$$(22)\quad E(l_\Delta) = \iiint L_\infty(1-e^{-K(\Delta+\tau)})q^{\text{true}}(L_\infty,K,\tau)dL_\infty dK d\tau$$

$$(23)\quad E(l_\Delta^2) = \iiint L_\infty^2(1-e^{-K(\Delta+\tau)})^2 q^{\text{true}}(L_\infty,K,\tau)dL_\infty dK d\tau.$$

Because we have assigned a unique code to each animal, we can also estimate from our pair of length measurements the powerful joint moment

$$(24)\quad E(l_0\cdot l_\Delta) = \iiint L_\infty^2(1-e^{-K\tau}) \times (1-e^{-K(\Delta+\tau)})q^{\text{true}}(L_\infty,K,\tau)dL_\infty dK d\tau.$$

Using the MCE methodology to infer a unique posterior pdf $q^{\text{mce}}(L_\infty,K,\tau)$, we can immediately write the form of the MCE posterior density:

$$\begin{aligned}(25)\quad q^{\text{mce}}(L_\infty,K,\tau) = p(L_\infty,K,\tau)\cdot\exp\{&\beta_0 \\ &+ \beta_1\cdot L_\infty(1-e^{-K\tau}) \\ &+ \beta_2\cdot L_\infty^2(1-e^{-K\tau})^2 \\ &+ \beta_3\cdot L_\infty(1-e^{-K(\Delta+\tau)}) \\ &+ \beta_4\cdot L_\infty^2(1-e^{-K(\Delta+\tau)})^2 \\ &+ \beta_5\cdot L_\infty^2(1-e^{-K\tau})(1-e^{-K(\Delta+\tau)})\}.\end{aligned}$$

The MCE posterior probability density function of the von Bertalanffy parameters is explicitly determined when the Lagrange multipliers are adjusted so as to exactly reproduce the measured moments corresponding to the constraints.

General MCE inversion methods can become computationally expensive in dimensions higher than two. It is of practical interest to consider when this trivariate problem can be reduced to two dimensions. In many mark–recapture experiments, the distribution of ages at time zero can be considered to be independent of the other two von Bertalanffy parameters and perhaps even known or manipulated.

If it can be justified that the distribution of ages at time zero is independent of the other parameters and can be known a priori, the five constraints corresponding to the measured moments can be rewritten

$$(26)\quad E(l_0) = \iint L_\infty(1-\nu_1(K))q^{\text{true}}(L_\infty,K)dL_\infty dK$$

$$(27)\quad E(l_\Delta) = \iint L_\infty(1-e^{-K\Delta}\nu_1(K))q^{\text{true}}(L_\infty,K)dL_\infty dK$$

$$(28)\quad E(l_0^2) = \iint L_\infty^2(1-2\nu_1(K)+\nu_2(K))q^{\text{true}}(L_\infty,K)dL_\infty dK$$

$$(29)\quad E(l_\Delta^2) = \iint L_\infty^2(1-2e^{-K\Delta}\nu_1(K)+e^{-2K\Delta}\nu_2(K)) q^{\text{true}}(L_\infty,K)dL_\infty dK$$

$$(30)\quad E(l_0\cdot l_\Delta) = \iint L_\infty^2(1-\nu_1(K)-e^{-K\Delta}\nu_1(K)+e^{-K\Delta}\nu_2(K)) \times q^{\text{true}}(L_\infty,K)dL_\infty dK$$

where

$$(31)\quad \nu_1(K) = E_\tau(e^{-K\tau})$$

and

$$(32)\quad \nu_2(K) = E_\tau(e^{-2K\tau})$$

which by our assumptions are known quantities.

For example, if the age distribution at time slice 0 is uniformly distributed between ages a^- and a^+, then

$$(33)\quad \nu_1(K) = \frac{(e^{-Ka+}-e^{-Ka-})}{K(a^+-a^-)}$$

and

$$(34)\quad \nu_2(K) = \frac{(e^{-2Ka+}-e^{-2Ka-})}{2K(a^+-a^-)}.$$

In any case the MCE posterior pdf takes the form

$$(35)\quad q^{\text{mce}}(L_\infty,K,\tau_0) = p(L_\infty,K)\cdot q_\tau^{\text{known}}(\tau)\cdot\exp\{\beta_0 + \beta_1\cdot L_\infty(1-\nu_1(K)) + \beta_2\cdot L_\infty^2(1-2\nu_1(K)+\nu_2(K)) + \beta_3\cdot L_\infty K(1-e^{-K\Delta}\nu_1(K)) + \beta_4\cdot L_\infty^2(1-2e^{-K\Delta}\nu_1(K)+e^{-2K\Delta}\nu_2(K)) + \beta_5\cdot L_\infty(1-\nu_1(K)-e^{-K\Delta}\nu_1(K)+e^{-K\Delta}\nu_2(K))\}$$

and as before, we must adjust the Lagrange multipliers until the MCE posterior density reproduces the given moments.

Example 6

Burnet (1969) has studied the growth of freshwater eels in New Zealand with a mark–recapture methodology. Data for *Anguilla australis* was hand-digitized from Fig. 2 in Burnet's paper to estimate the mean, standard deviation, and correlation of the length at first capture, and the length a year later, and are summarized in Table 3. Under the assumptions of a uniform prior density and a hypothesized negative exponential age distribution at first capture (with mean age = 8.5 yr), the estimated pdf of the von Bertalanffy parameters is presented in Fig. 8, in which some negative diagonal structure can be observed.

Discussion

The MCE formalism, which we have here applied to the problem of determining the distribution of the von Bertalanffy parameters, exploits the variations in the information about $q^{\text{true}}(L_\infty,K,t_0)$ implied by projection through different integral kernel functions. The concept developed in this paper can be extended to any deterministic growth model that can represent the growth of an individual animal.

The strengths and weaknesses of the MCE approach lie in the ability to insert background knowledge of unknown applicability into the problem by way of the prior pdf. Examination of equation 11 shows that the posterior pdf is in the form of the prior pdf multiplied by an exponential distortion factor. If the prior pdf is a good guess, then the magnitude of the Lagrange parameters will be small and the analytic degrees of freedom of the model will be spent "fine-tuning" the posterior pdf, explaining what is not already known about the system under study. If the prior pdf is not a good guess, the magnitude of the Lagrange parameters will be large as the degrees of freedom of the distortion function are spent overcoming the unrepresentativeness of the prior pdf. It should be generally noted that if the hypothesized prior $p(L_\infty,K,t_0)$ happens to be identical to the true pdf $q^{\text{true}}(L_\infty,K,t_0)$, then $\beta_1 = 0$, $\forall_i$ and $q^{\text{mce}}(L_\infty,K,t_0) = p(L_\infty,K,t_0) = q^{\text{true}}(L_\infty,K,t_0)$.

As the number of measured moments m_i increases, the MCE procedure can overcome any specification of the prior pdf so long as $p(L_\infty,K,t_0) > 0$ everywhere. In the information theory literature, this appealing behavior of the MCE inverse is termed the "washing out" of old uncertain information with new facts. Whenever there is an inconsistency between the prior $p(I)$ and the actual data, the new data take precedence.

The MCE inverse methodology can be viewed as a formal way to deal with missing information problems by adapting the form of the model to the available moments. The kernels corresponding to missing moments are simply not present in the argument of the exponential function in equations 8 and 18.

It is a "method of moments" inverse technique. That is, the Lagrange parameters $\{\beta_i\}$ are defined, not statistically estimated. Sampling variability in the measured moments will be propagated through to the posterior density $q(I)$.

Practical implementation of the MCE methodology generally relies on some kind of iterative nonlinear minimization procedure. Convergence can be accelerated if either $p(L_\infty,K,t_0)$ is a very good guess or if a good starting value for $\vec{\beta}$ is chosen. One method of quickly estimating a reasonable starting value is to assume that $\vec{\beta}$ is small enough that the multiplicative exponential distortion factor in equation 11 can be replaced with a Taylor series linearization about the origin. We can then write an approximate expression for the MCE posterior as

$$(36)\quad q^{\text{mce}}(\vec{x};\vec{\beta}) = p(\vec{x})[1+\sum_i^M \beta_i f_i(\vec{x})]$$

which can be fit to the moments using linear mathematics.

This form is suggestive because it closely resembles a class of pdf estimators based on orthogonal function expansions that may be computed very efficiently. If $p(\vec{x})$ is multivariate Gaussian, and $f_i(\vec{x})$ are appropriately chosen multivariate Hermite polynomials, then equation 36 is the well-known Hermite orthogonal expansion of the pdf. Similarly, if $p(\vec{x})$ is multivariate exponential, multivariate Laguerre polynomials form a convenient orthogonal expansion. A future research direction is to explore the adequacy of these pdf estimates of the von Bertalanffy parameters, which are suboptimal approximations in the cross-entropy sense, but which can be estimated with significantly less computation than the general MCE form.

Estimation Issues

It has been stressed that the MCE inversion procedure is a "method of moments" where summaries of sampled data are assumed somewhat arbitrarily to be equivalent to asymptotic expected values, from which the Lagrange parameters are defined rather than statistically estimated. Anyone who has participated in fisheries research data collection or has had the responsibility of summarizing such data would be justifiably concerned about this suppression of uncertainty. The attempt to make this pdf approximation scheme better suited for practical problems is an active research topic.

The MCE posterior density is the optimal solution to a calculus of variations problem where the moments are represented as integral equality constraints on the unknown true density. It is also possible to formulate this problem using integral inequality constraints. For example, instead of using the equality constraint

$$(37)\quad m_i = \int f_i(L_\infty,K,t_0)q^{\text{true}}(L_\infty,K,t_0)dL_\infty dK dt_0,$$

two inequality constraints might be written:

$$(38)\quad m_i + 2\frac{\sigma_i}{\sqrt{N_i}} > \int f_i(L_\infty,K,t_0)q^{\text{true}}(L_\infty,K,t_0)dL_\infty dK dt_0$$

$$(39)\quad m_i - 2\frac{\sigma_i}{\sqrt{N_i}} < \int f_i(L_\infty,K,t_0)q^{\text{true}}(L_\infty,K,t_0)dL_\infty dK dt_0.$$

That is, confidence intervals based on some reasonable assessment of the variability of the moments due to sampling are employed to constrain the class of consistent densities. Kullback's Principle can still be applied to the now larger convex set of pdfs satisfying the given inequality constraints.

Until a satisfactory method is found to analytically determine the effect of moment estimation error on the posterior pdf, computationally expensive resampling methods of assessing the variability, such as jackknifing and bootstrapping (Efron 1982), can be employed.

Conclusion

The problem of determining of the general joint distribution of the parameters of the von Bertalanffy growth model can be approached as an ill-posed inverse problem. MCE inversion techniques allow the selection of a reasonable unique solution, directly incorporating background information when available.

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Appendix A: Convexity

It is easily shown that the class C of probability density functions consistent with a given set of moment constraints is a convex set. Suppose that there exist two densities, $p_1(\vec{x}) \in C$ and $p_2(\vec{x}) \in C$, such that

$$p_1(\vec{x}) \neq p_2(\vec{x}). \tag{40}$$

By definition of membership in C:

$$m_k = \int f_k(\vec{x}) p_1(\vec{x})\, d\vec{x} \tag{41}$$

and

$$m_k = \int f_k(\vec{x}) p_2(\vec{x})\, d\vec{x}. \tag{42}$$

To show convexity, it is sufficient to demonstrate that

$$p(\vec{x}) = a \cdot p_1(\vec{x}) + (1-a) \cdot p_2(\vec{x}) \in C \quad \forall a \ni 0 \leqslant a \leqslant 1. \tag{43}$$

But

$$\begin{aligned} \int f_k(\vec{x}) p(\vec{x})\, d\vec{x} &= a \int f_k(\vec{x}) p_1(\vec{x})\, d\vec{x} + \\ &\quad (1-a) \int f_k(\vec{x}) p_2(\vec{x})\, d\vec{x} \\ &= a \cdot m_k + (1-a) \cdot m_k \\ &= m_k \quad 0 \leqslant k \leqslant m. \end{aligned}$$

Therefore

$$p(\vec{x}) = a \cdot p_1(\vec{x}) + (1-a) \cdot p_2(\vec{x}) \in C \quad \forall a \ni 0 \leqslant a \leqslant 1. \tag{45}$$

Appendix B: Derivation of the Form of the MCE Posterior Density

Cross-entropy minimization is a general procedure for approximating a true but unknown probability density function $q'(x)$ given a set of moments and a prior assessment $p(x)$. The approximating posterior $q(x)$ is chosen such that of all distributions consistent with the known moments, we select the one most similar to the prior model. If the assumptions are specific and the set of measured moments is not internally contradictory, the posterior $q(x)$ thus obtained is unique.

The logic of Kullback's Principle would have us find the function $q(\vec{x})$ that minimizes

$$(46)\quad H[q(\vec{x}),p(\vec{x})] = \int q(\vec{x})\log\frac{q(\vec{x})}{p(\vec{x})}\,d\vec{x}$$

while exactly satisfying the set of constraint equations

$$(47)\quad m_j = \int f_j(\vec{x})\cdot q(\vec{x})\,d\vec{x} \quad j=1,\ldots,M.$$

An Isoperimetric Calculus of Variations Problem

All of the MCE problems addressed in this paper have a common structure, which may be addressed with calculus of variations techniques. We are given a set of constraints $\{m_j\}$ which are known to satisfy the following definite integral equation:

$$(48)\quad m_j = \int g_j[q(\vec{x})]\,d\vec{x}$$

where $q(\vec{x})$ is a function to be determined. We are also given a measurement functional, again a definite integral:

$$(49)\quad f_{\text{meas}}[q(\vec{x})] = \int I_{\text{meas}}[q(\vec{x})]\,d\vec{x}$$

and we want to obtain the $q(\vec{x})$ that extremizes $F_{\text{meas}}[q(\vec{x})]$.

In optimization theory, applications with this form are called "isoperimetric" calculus of variations problems. The name derives from the classical problem of finding the function with the maximum enclosed area given a fixed length boundary or perimeter.

To solve this problem, we use the Lagrange multiplier method (Weinstock 1952), forming the equation

$$(50)\quad Q[q(\vec{x});\vec{\beta}] = I_{\text{meas}}[q(\vec{x})] + \sum_{j=1}^{M}\beta_j g_j[q(\vec{x})].$$

We now minimize this equation with respect to $q(\vec{x})$. Taking the derivative and setting it equal to zero,

$$(51)\quad \frac{dQ}{dq} = 0,$$

we derive an expression that $q(\vec{x})$ can only satisfy at an extremum of $Q[q(\vec{x});\vec{\beta}]$. We must then verify that the extremum is in fact a minimum by checking the higher order derivatives.

Application to the MCE Problem

For the MCE problem, we can identify

$$(52)\quad I_{\text{meas}} = q(\vec{x})\log\frac{q(\vec{x})}{p(\vec{x})}$$

and

$$(53)\quad g_j = f_j(\vec{x})\cdot q(\vec{x}).$$

Therefore

$$(54)\quad Q[q(\vec{x});\vec{\beta}] = q(\vec{x})\log\frac{q(\vec{x})}{p(\vec{x})} + \sum_{j=1}^{M}\beta_j f_j(\vec{x})q(\vec{x}) + \lambda_0 q(\vec{x}).$$

The last term reflects the fact that we usually have the constraint

$$(55)\quad \int q(\vec{x})\,d\vec{x} = 1$$

as well because $q(\vec{x})$ must be a valid normalized probability density function.

Taking the first derivative with respect to $q(\vec{x})$, we derive

$$(56)\quad \frac{dQ}{dq} = \log\frac{q(\vec{x})}{p(\vec{x})} + 1 + \lambda_0 + \sum_{j=1}^{M}\beta_j f_j(\vec{x})$$

and for the second derivative we obtain

$$(57)\quad \frac{d^2Q}{dq^2} = \frac{1}{q(\vec{x})}.$$

Setting the first derivative equal to zero:

$$(58)\quad \log q(\vec{x}) = \log p(\vec{x}) - 1 - \lambda_0 - \sum_{j=1}^{M}\beta_j f_j(\vec{x}).$$

Calling $\beta_0 = \lambda_0 + 1$ and $f_0(\vec{x}) = 1$ for all $\vec{x}$, we can write

$$(59)\quad \log q(\vec{x}) = \log p(\vec{x}) - \sum_{j=0}^{M}\beta_j f_j(\vec{x}).$$

Therefore

$$(60)\quad q(\vec{x}) = p(\vec{x})\cdot\exp\left\{-\sum_{j=0}^{M}\beta_j f_j(\vec{x})\right\}$$

which is the classical MCE posterior density (Johnson 1979; Shore and Johnson 1980).

Inserting this solution into the expression for the second derivative, we see that the positivity of the prior density $p(\vec{x})$ implies the positivity of $q(\vec{x})$, which guarantees that the second derivative is positive at the solution point. Hence, the solution is a minimum as desired.

Effect of Stochasticity on Optimal Harvesting Strategies in Some Lumped-Parameter Fishery Models

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Lovejoy, W. S. 1988. Effect of stochasticity on optimal harvesting strategies in some lumped-parameter fishery models. Can. J. Fish. Aquat. Sci. 45: 1789–1800.

This paper introduces some methods for anticipating the difference between optimal harvesting strategies in a fishery model with stochastic recruitment and in the corresponding deterministic model with recruitment equal to its expected value. It extends known results on the sign of the difference and presents ways to estimate the magnitude. Two classes of lumped-parameter models are discussed. In myopic models, the policy difference is likely to be insignificant. In more general models with downward sloping demand for fish and increasing marginal cost of fishing effort, a heuristic measure is introduced that can suggest the direction and magnitude of the policy shift.

Le présent document présente certaines méthodes permettant de prévoir la différence entre les stratégies de récolte optimale dans un modèle d'exploitation des pêches à recrutement stochastique et le modèle déterministe correspondant dont le recrutement est égal à la valeur prévue. Il porte les résultats connus sur le signe de la différence et présente des moyens pour évaluer l'ampleur. On examine deux classes de modèles à paramètre localisé. Dans le cas de modèles myopes, la différence de politique risque d'être peu importante. Dans le cas de modèles plus généraux avec une demande à la baisse de poisson et un coût marginal accru de l'effort de pêche, on introduit une mesure heuristique qui peut indiquer l'orientation et l'ampleur du changement de politique.

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It is generally conceded that randomness plays a major role in the dynamics of fish populations. This has fostered a considerable research effort to find optimal or near-optimal harvesting policies in stochastic fishery models (cf. Jaquette 1972; Reed 1978; Mendelssohn 1978, 1980; Mendelssohn and Sobel 1980; and references therein). This literature typically assumes that the stock dynamics are stochastic with known distributions for the random parameters. It is an unfortunate fact that these distributions are seldom known in actual fisheries. One possible resolution of this issue is to adopt harvesting policies that are designed to reveal information about the unknown parameters when it is economically warranted to do so (cf. Mendelssohn 1980; Walters 1981; Smith and Walters 1981; and references therein). Solution procedures for finding such a policy can be laborious. If the mean of the recruitment function is known, another possibility is to use a policy appropriate for a deterministic model (recruitment is set to its expected value with probability one) as an approximate policy for the stochastic fishery. Reed (1979), Lewis (1981), and Lovejoy (1986a) considered the directional policy shift that results from such an approximation, but did not address its magnitude. In a related paper, Vincent (1987) bounded the perturbations that will call for additional control effort to recapture a deterministic equilibrium solution, presuming this is desirable.

This paper introduces some methods for anticipating the direction and magnitude of the difference between optimal harvesting strategies in fishery models with stochastic recruitment and in the corresponding deterministic model with recruitment set equal to its expected value. The models analyzed assume that a deterministic model is knmown and then allow one to introduce additive or multiplicative randomness in the recruitment function.

The two most restrictive assumptions that are imposed in the paper are (1) the fishery can be appropriately represented by a lumped parameter model, i.e. all ages and sexes are aggregated into a single number such as population or biomass, and (2) the mean of the recruitment distribution is known with certainty. The deficiencies of lumped-parameter models are well known (cf. Clark 1976; Mendelssohn 1978). Unfortunately, realistic age-structured models that include stock dependent recruitment can be analytically intractable, and the hope is that the more transparent lumped-parameter representation will offer some insights relevant to the more complicated biological system. The tractability problem explains the prevalence of lumped-parameter models in the literature. The assumption that the mean of the recruitment function is known with certainty is also unrealistic. Historical stock–recruitment data typically offer only gross estimates for the relationship between escapement levels and future stock sizes, and this only after imposing additional assumptions such as stationarity of this relationship. It is true, however, that the mean of such a relationship will be known with greater precision than the variance or any higher moment (due to the nature of standard estimation techniques, see Kendall and Stuart 1979) and that the mean, however estimated, dominates the calculations of practitioners. Again, this latter development is driven by tractability in that the mean is the highest confidence estimate one usually has to work with.

The lumped-parameter models analyzed here allow for the introduction of random parameters that either additively or multiplicatively affect an otherwise deterministic recruitment function. It is possible that the modelling framework of a deterministic model with additive or multiplicative random perturbations is not the appropriate paradigm for real fisheries. It is probably an historical coincidence that these models pervade the literature, since the more tractable deterministic models were analyzed first and then these were altered to consider stochasticity. Still, it is common in practice to suggest harvesting policies based upon essentially deterministic calculations using the expected values of random parameters, i.e. assume a deterministic model. Then, in policy deliberations, the prescriptions of these models are challenged for not including randomness. This paper is designed to answer this charge. If a deterministic model, however derived, is an historical basis for management, then how much randomness can one introduce into this model before the policy prescriptions change dramatically? The paper thus responds to the question posed by Clark (1985): by what percentage should the deterministic escapement be altered in the presence of uncertainty?

The paper shows that Reed's (1979) harvesting model belongs to the more general class of myopic models (Sobel 1981). Reed's directional results are extended to this class, and it is argued that the magnitude of the policy shift is likely to be minimal for myopic models. More general models are then considered, and a heuristic measure is introduced that can bound the policy shift between the deterministic and stochastic models. This measure can be explicitly calculated from the solution to the deterministic model and the variance of the recruitment random variable. Consequently, if the mean recruitment is known but moments higher than the mean are known with less precision, direct use of the measure using confidence limits for the variance will yield confidence limits for the prescribed policy change. In the extreme, suppose mean recruitment is known but no information regarding moments higher than the mean is available. In this case the measure can be used to calculate a threshold variance below which the policy changes will be less than any desired limit. This gives an efficient indication of how much stochasticity can be introduced into the model before policy prescriptions must be altered.

The policy changes predicted by the measures introduced in this paper are likely to be conservative in that they will overpredict the actual policy change. This is because the measures are designed to bound the policy shift for any distribution of the random parameter, even if this is skewed or bimodal. The shift appropriate for the more well-behaved distributions (e.g. normal) may be less dramatic. Thus, one can expect the appropriate policy shift to be equal to or less than that predicted by these measures. The most prudent uses of these measures, then, are as conservative estimates.

Finally, the measures depend upon the present stock level, and consequently can be used to identify those stock levels at which the optimal policy is most sensitive to stochastic shocks. For example, a fishery may call for a harvesting policy that is less sensitive to stochasticity at high stock levels than at low ones, and the heuristic measures should indicate this.

These points are clarified in the discussion below. The general model is introduced, myopic models are considered, and a more general class of models and the heuristic measures are introduced. Some example applications are then given.

Model Description

This paper considers fishery harvesting problems that can be modeled as lumped-parameter discrete-time sequential decision processes. Specifically, let $x(t)$ denote the stock size or biomass of the fish stock at the beginning of the fishing season in time period t and $y(t)$ the escapement, i.e. the stock or biomass remaining at the end of that season t.

At the beginning of each season the manager can observe the stock $x(t)$ and choose an escapement $y(t) \leq x(t)$ (hence $x(t) - y(t)$ will be harvested during the period). Society then receives a reward $r(x(t),y(t))$, representing the net social benefit for the season's harvesting activities, and the next season begins with stock level $x(t+1) = f(y(t),D(t))$ where $D(t)$ is a random variable generated each period from a stationary probability distribution.

Returns in period t are discounted by a factor α^t, where $\alpha \in [0,1)$. The objective is to observe x and choose y so as to maximize the expected sum of the discounted returns over an infinite time horizon. A *policy* is a function $y = \delta(x)$ = a specified feasible escapement from stock level x. That is, given any state x, a policy tells us which escapement level to choose. We seek a policy that attains the maximum of

$$(1) \quad E \sum_{t=1}^{\infty} \alpha^{t-1} r(x(t),\delta(x(t)))$$

where $x(t+1) = f(\delta(x(t)),D(t))$, $x(0)$ is given, and E denotes the expectation. We shall assume throughout that all functions have as many continuous derivatives as we need. The optimal policy can be found by a standard successive approximation algorithm (cf. Bertsekas 1976). Let $V(x)$ denote the value of starting the decision problem with stock level x and following some specified harvesting policy. Then

$$(2) \quad J(x,y,V) = r(x,y) + \alpha E V(f(y,D))$$

is the value of starting with stock level x, choosing escapement y, and then following the specified policy starting with the subsequent fishing season.

Then starting with any $V_0(x)$ and defining

$$(3) \quad V_t(x) = \max\{J(x,y,V_{t-1}) : y \leq x\},$$

the sequence of functions $\{V_t\}$ will converge to an optimal value function $V^*(x)$ (i.e. the value of following the optimal policy), and any action y that attains the maximum in $J(x,y,V^*)$ over $y \leq x$ will be an optimal action at x, i.e. $\delta^*(x) = y$ is optimal.

This paper considers recruitment relationships of the form

Additive stochasticity: $f(y,D) = g(y) + D$ where $E(D) = 0$
Multiplicative stochasticity: $f(y,D) = Dg(y)$ where $E(D) = 1$.

Note that in both cases, $g(y)$ is the expected recruitment given escapement y, i.e. $E\{f(y,D)\} = g(y)$ for both additive and multiplicative stochasticity.

The results below allow one to anticipate the difference in the optimal policy between the model with deterministic recruitment $g(y)$ and that with stochastic recruitment $f(y,D)$. Specifically, if one solves the deterministic program characterized by $J(x,y,V) = r(x,y) + \alpha V(g(y))$, how will the optimal policy for this deterministic problem, $\delta_d^*(x)$, differ from the optimal policy for the stochastic problem, $\delta_s^*(x)$? Note that we require an answer for this question that is independent of the precise nature of the random variable D, since only its expected value is assumed known. The usefulness of the results established in the paper is that we need only solve the known deter-

ministic problem to say something about the unknown stochastic policy δ_s^*. Of special interest are systems for which δ_s^* approximately equals δ_d^*, i.e. stochasticity is not important in determining policy. This situation is called "certainty equivalence" in the control theory literature (cf. Bertsekas 1976). Two special classes of the general model will be considered. The next section considers myopic models and the subsequent section considers more general models with some structural assumptions on the functions r and g.

Myopic Models

Reed (1979) demonstrated the directional effects of multiplicative stochasticity in a class of harvesting models with rewards r that separate into state- and action-dependent components. Here it is shown that Reed's model falls within the more general framework of myopic programs outlined in Sobel (1981). This observation simplifies the proofs of many of Reed's results and permits analysis of additive stochasticity in an equally straightforward manner. At the end of this section it is argued that for models with constant price of fish, constant marginal cost of effort, Cobb–Douglas production functions, and myopic optima, one might expect stochasticity to have little effect on the optimal harvest levels.

Sobel (1981) showed that if r can be expressed as the sum of functions of the state and action, i.e. $r(x,y) = L(x) + K(y)$, then

$$(4)\quad E\sum_{t=1}^{\infty}\alpha^{t-1}r(x(t),y(t)) = L(x(1)) + E\sum_{t=1}^{\infty}\alpha^{t-1}\Gamma(y(t))$$

where $\Gamma(y) = K(y) + \alpha EL(f(y,D))$. Detailed structural results for models of this form can be found in Mendelssohn and Sobel (1980) and Sobel (1981). The discussion to follow uses the following:

Proposition 1: If Γ has a global maximum at y^*, and $f(y^*,D) \geq y^*$ with probability one, then $\delta^*(x) = y^*$ for all $x \geq y^*$.

Proof: This is Sobel (1981) Theorem 1.

Note that under the conditions of Proposition 1, y^* is easily found by a one-step maximization of Γ, without solving the dynamic program recursively. Thus we can easily characterize the optimal policy for states $x \geq y^*$. Note that once x exceeds y^*, under the conditions of Proposition 1 it can never again fall below y^* if an optimal policy is followed. Specifically, if the initial stock level exceeds y^*, then the optimal action is to harvest down to y^* each time period. The conditions of Proposition 1 are those for a "myopic optimum" (Sobel's terminology), so named because the relatively simple single stage maximization of Γ on S suffices to characterize the optimal policy for $x \geq y^*$ in the infinite-horizon sequential decision problem. The property that $f(y^*,D) \geq y^*$ with certainty is termed "repeatability" by Sobel and refers to the fact that for any $x \geq y^*$, harvesting down to y^* will be feasible each subsequent time period. Reed calls a repeatable y^* "self-sustaining."

The effects of stochasticity are easily deduced in myopic models.

Define

$$(5)\quad \begin{aligned}\Gamma_d(y) &= K(y) + \alpha L(f(y,E(D))) = K(y) + \alpha L(g(y))\\ \Gamma_s(y) &= K(y) + \alpha EL(f(y,D))\end{aligned}$$

and let y_d^* and y_s^* be the respective maximizing arguments on S. Then under conditions of repeatability, y_d^* and y_s^* will characterize the optimal policies in the deterministic and stochastic models, respectively. If $d\Gamma_d/dy \geq (\leq, =)\ d\Gamma_s/dy$ for all y, then $y_d^* \geq (\leq, =)\ y_s^*$. Suppose that $\partial/\partial y\{L(f(y,D))\}$ is convex in D. Then from Jensen's inequality $d\Gamma_d/dy = dK/dy + \alpha\partial/\partial y\{L(f(y,E(D)))\} \leq dK/dy + \alpha E\partial/\partial y\{L(f(y,D))\} = d\Gamma_s/dy$, so $y_s^* \geq y_d^*$. If the conditions of Proposition 1 are satisfied, then $\delta_s^*(x) \geq \delta_d^*(x)$ for all $x \geq y_s^*$, i.e. stochasticity makes us more conservative. If $\partial/\partial y\{L(f(y,D))\}$ is concave in D, similar reasoning yields $y_s^* \leq y_d^*$ and for myopic optima $\delta_s^*(x) \leq \delta_d^*(x)$ for $x \geq y_d^*$, i.e. stochasticity makes us more liberal. If $\partial/\partial y\{L(f(y,D))\}$ is linear in D, then myopic optima will exhibit certainty equivalence for $x \geq y_d^* = y_s^*$.

As an example, consider the reward function proposed by Reed:

$$(6)\quad r(x,y) = p(x-y) - \int_y^x c(u)du$$

where p is the constant price of fish and $c(x)$ is the marginal cost of harvest at stock level x. In this case:

$$r(x,y) = px - py - \int_0^x c(u)du + \int_0^y c(u)du$$

and

$$(7a)\quad L(x) = px - \int_0^x c(u)du$$

$$(7b)\quad K(y) = -py + \int_0^y c(u)du.$$

If $c(u) \to \infty$ as $u \to 0$, then we will never harvest to zero (incurring infinite cost) and we can redefine the integrals (7) to eliminate no meaningful policies (see Reed).

A Cobb–Douglas production function for harvest is

$$(8)\quad dx/dt = -qEx^{\theta}$$

where $\theta \geq 0$, q is a constant, and E is fishing effort. The constant q can be interpreted as a constant catchability coefficient, or one can model catchabilities that depend geometrically on stock by $dx/dt = -qx^nEx^m = qEx^{\theta}$ where $\theta = n + m$, as shown by Reed. This type of production function is consistent with marginal cost of fish $c(x) = k/x^{\theta}$, where $k = c_e/q$ and c_e is the constant marginal cost of effort. $\theta = 1$ implies a Schaefer production function, $c(x) = k/x$.

For models in this class (recall $g(y) = E\{f(y,D)\}$):

$$\Gamma_d(y) = -py + \int_0^y c(u)du + \alpha pg(y) - \alpha\int_0^{g(y)} c(u)du$$

$$\Gamma_s(y) = -py + \int_0^y c(u)du + \alpha pg(y) - \alpha E\int_0^{f(y,D)} c(u)du.$$

Hence, letting $\beta(y) = c(g(y))g'(y) - Ec(f(y,D))f'(y,d)$ where the prime denotes the partial derivative with respect to y, we have upon differentiation under the expectation $d\Gamma_s/dy = d\Gamma_d/dy + \alpha\beta(y)$. The basic result for the directional effects of stochasticity is Proposition 2.

Proposition 2:

(a) For the additive stochastic model if $c(x)$ is convex (concave, linear), then y_s^* is $\leq (\geq, =)\ y_d^*$.

(b) For the multiplicative stochastic model if $xc(x)$ is convex (concave, linear), then y_s^* is $\leq (\geq, =)\ y_d^*$.

Proof:

(a) $\beta(y) = g'(y)[c(g(y)) - Ec(g(y) + D)]$ is $\leq (\geq, =)\ 0$ if $c(x)$ is convex (concave, linear).

(b) $\beta(y) = g'(y)[c(g(y)) - EDc(Dg(y))]$ is $\leq (\geq, =)\ 0$ if $xc(x)$ is convex (concave, linear).

Part b of Proposition 2 reproduces portions of Theorem 3 in Reed. In particular, for myopic optima with $c(x) = k/x^{\theta}$, multiplicative stochasticity will make us more conservative if $0 < \theta < 1$, more liberal if $\theta > 1$, and stochasticity will have no effect if $\theta = 1$ (Schaefer model) or $\theta = 0$ (constant marginal

TABLE 1. Distributions for D used in myopic models.

No.		Probability mass function									
						Additive					
1	D_i	−20	−15	−10	−5	−2	2	5	10	15	20
	Prob_i	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
2	D_i	−10	−8	−6	−4	−2	2	4	6	8	10
	Prob_i	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
3	D_i	−20	−15	−10	−8	−2	2	5	9.75	10	
	Prob_i	0.07	0.07	0.07	0.07	0.07	0.2	0.2	0.2	0.2	
4	D_i	−10	−9.75	−5	−2	2	8	10	15	20	
	Prob_i	0.05	0.2	0.2	0.2	0.07	0.07	0.07	0.07	0.07	
Multiplicative											
1	D_i	0.3	0.5	0.7	0.8	0.9	1.1	1.2	1.3	1.5	1.7
	Prob_i	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
2	D_i	0.5	0.6	0.7	0.8	0.9	1.1	1.2	1.3	1.4	1.5
	Prob_i	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
3	D_i	0.4	0.5	0.6	0.7	0.9	1.2046				
	Prob_i	0.07	0.07	0.07	0.07	0.07	0.65				
4	D_i	0.7954	1.1	1.3	1.4	1.5	1.6				
	Prob_i	0.65	0.07	0.07	0.07	0.07	0.07				

TABLE 2. Results from myopic experiments.

Distribution No.	No. of cases with repeatability	$\Delta^* < -1$	$\Delta^* = -1$	$\Delta^* = 0$	$\Delta^* = 1$	$\Delta^* > 1$
1 (additive)	97	0	1	96	0	0
1 (multiplicative)	74	0	0	74	0	0
2 (additive)	87	0	1	86	0	0
2 (multiplicative)	80	0	0	79	1	0
3 (additive)	77	0	1	76	0	0
3 (multiplicative)	69	0	0	67	2	0
4 (additive)	67	0	2	65	0	0
4 (multiplicative)	67	0	0	67	0	0

cost of fish). Additive stochasticity will always make us liberal unless $\theta = 0$, in which case stochasticity has no effect.

The above results give some insight into the directional effects of stochasticity for myopic models. To infer the magnitude of the shift, $\Delta^* = y_s^* - y_d^*$, it is an easy matter to maximize Γ_s for a range of plausible distributions that maintain repeatability. We now show that this exercise would likely reveal near certainty equivalence for Cobb–Douglas models. Using a quadratic Taylor series expansion about $g(y_d^*)$ for $c(x) = k/x^\theta$, it is shown in Appendices A and B that for both additive and multiplicative stochasticity (the latter demonstration is restricted to $\theta \in [0,2]$, a reasonable range to consider) $\beta(y)$ is not likely to contribute significantly to the expressions for Γ'_d and Γ'_s, i.e. we can expect near certainty equivalence.

To test this claim, over 290 random problems were generated using the Beverton–Holt recruitment function $g(y) = ay/(1 + by)$. Parameters were generated randomly (using the random number generator on an IBM PC) on the following intervals: $\theta \in [0,2]$, $k \in [0,25]$, $p \in [0,25]$, $\alpha \in [0.5,1]$, $a \in [0,25]$, and b was set equal to $(a\text{-}1)/100$ so that $g(100) = 100$. S was assumed to be [1,100] and the randomly generated Γ_d function was maximized over $y = 1,2,\ldots,100$. Then the analogous Γ_s functions were maximized using a variety of input distributions for both the additive and multiplicative stochastic models. The distributions used are shown in Table 1 and the results for $\Delta^* = y_s^* - y_d^*$ are reported in Table 2. Note that with Γ being tested at discrete y values on S, the calculated Δ^* will be restricted to integer values, i.e. finer resolution is lost. Models that lost repeatability were discarded. In no case did $|\Delta^*|$ exceed unity, and $\Delta^* = 0$ in 98.5% of the additive and 99% of the multiplicative cases.

One possible intuitive explanation for this phenomenon hinges upon why we might react significantly to stochasticity. Stochasticity may affect policy if it can put us unintentionally in a calamitous state from which escape is slow or impossible. Shocks that give us more fish than expected are not much cause for concern because we can harvest down to wherever we please. In contrast, shocks that put us unintentionally in a low population, low growth rate state (an extreme example in extinction) are to be feared because returns are low and escape is slow or impossible.

However, the assumption of repeatability prevents this type of dire development, since $f(y^*,D) \geq y^*$ with certainty. With stock robustness guaranteed the dramatic effects of stochastic-

ity are eliminated, and we are left with the adjustments to marginal costs and revenues that stochasticity induces. With constant price of fish, constant marginal cost of effort, and a Cobb–Douglas production function, these effects are most likely minimal, as shown above.

Random variation in myopic models therefore appears to be innocuous, except when it is large enough to cause lack of repeatability. It is to this problem that we now turn and to the consideration of models that do not have the myopic structure.

More General Models

In this section, a heuristic measure for the difference between the stochastic and deterministic optimal policies, $\Delta^*(x) = \delta_s^*(x) - \delta_d^*(x)$, will be derived. A preliminary definition is needed. A function $r(x,y)$ has "isotone differences" in x and y if for all $y \geq y'$, $r(x,y) - r(x,y')$ is nondecreasing in x. In this section it is no longer required that r separate into functions of the state and action, but it is assumed that in equation (2), $f(\ ,D)$ is nondecreasing (equivalently $g(\ )$ is nondecreasing) in y and $r(x,y)$ has isotone differences in x and y. This class of problems contains several interesting fishery models, as will be shown by example in the following section.

Suppose we solve the deterministic problem using the recursion (3) for the optimal policy $\delta_d^*(x)$ and optimal value function $V_d^*(x)$. The basic directional result is from Lovejoy (1986b).

Proposition 3: If $\partial/\partial y(V_d^*(f(y,D)))$ exists and is convex (concave, linear) in D, then there exists an optimal policy δ_s^* for the stochastic problem such that $\delta_s^*(x) \geq (\leq, =)\ \delta_d^*(x)$ for all x.

Proof: This is Lovejoy (1986b) Proposition 5 for differentiable functions.

It is shown in Appendix C that for interior solutions a heuristic approximation for the policy difference in additive models is $\Delta^*(x) \approx \Delta_a(x) = \lambda_a(x)\sigma^2$ where

$$(9)\quad \lambda_a(x) = \quad (1/2)\quad \frac{\alpha V''' g'}{|r'' + \alpha(g')^2 V''|}$$

and $V^{(n)} = \partial^n V_d^*/\partial x^n$ evaluated at $g(\delta_d^*(x))$, $g' = \partial g/\partial y$ evaluated at $\delta_d^*(x)$, $r'' = \partial^2 r/\partial y^2$ evaluated at x and $\delta_d^*(x)$, and $\sigma^2 =$ variance of D.

As demonstrated in Appendix C, this heuristic measure derives from local approximations to the functions r, g, and V and hence can be expected to be most accurate for low variance distributions. The use of this measure as a conservative estimate is appropriate for noninterior solutions, since constraints only serve to restrict motion. For example, if $\delta^*_d(x) = x$, i.e. we do not harvest, and $\Delta(x) > 0$, urging conservation, we would conclude that $\delta^*_s(x) = x$, as well, since higher escapements are infeasible.

For additive models, $\partial/\partial y V(f(y,D)) = \partial/\partial y V(g(y) + D) = [\partial/\partial x V(g(y) + D)]\ [\partial g(y)/\partial y]$ which will be convex (concave) in D if $\partial V/\partial x$ is convex (concave), i.e. if $\partial^3 V/\partial x^3$ is $\geq (\leq)$ zero. Since g' is nonnegative by assumption, the numerator in equation (9) will be $\leq(\geq, =)$ zero if Proposition 3 implies that $\Delta^*(x)$ is $\leq(\geq, =)$ zero. The denominator in equation (9) is an approximation to the second derivative with respect to y of $J(x,y,V_d^*)$ evaluated at x and $\delta_d^*(x)$. This should be nonpositive at an interior maximum, but need not be if the maximum occurs at a boundary of the feasible set. Hence, the absolute value is used so that the sign of $\Delta_a(x)$ will indicate the appropriate directional change, consistent with the rigorous results of Proposition 3. Estimating the magnitude of the change amounts to assessing how "convex" the partial derivative $\partial/\partial y[V_d^*(g(y) + D)]$ is. Arrow (1971, chap. 3) faced a similar problem in assessing how "risk averse" an individual is from his/her utility function. Arrow derived a measure of risk aversion that was essentially the second derivative of the utility function divided by the first derivative, the idea being to scale the change in slope by the absolute magnitude of the slope. $\Delta_a(x)$ from equation (9) has a similar interpretation in that the numerator is the second derivative with respect to D of the expression for which the "degree of convexity" is of interest, in this case, $\partial/\partial y[V_d^*(g(y)+D)]$, evaluated at $y = \delta_d^*(x)$ and $D = E(D) = 0$. The denominator is an approximation for $|\partial^2 J/\partial y^2|$ and serves the scaling function. From Proposition 3 if $V''' = 0$, then $\Delta^*(x) = 0$. Also, we have trivially that $\sigma^2 = 0$ will imply $\Delta^*(x) = 0$. Note that $\Delta_a(x) = \lambda_a(x)\sigma^2$ satisfies these intuitive conditions.

Note that the departure from certainty equivalence is proportional to the third-order behavior of the value function for the deterministic model. In particular, a quadratic value function will imply that additive stochastic shocks will not affect policy. This is consistent with known results for models with linear dynamics, quadratic reward functions, and additive stochasticity, where the value functions are known to be quadratic and certainty equivalence is known to hold (cf. Bertsekas 1976). For models lacking this structure, λ_a measures the departure from quadratic behavior in V^* and uses this to anticipate the departure from certainty equivalence in policy.

For multiplicative models, it is shown in Appendix D that $\Delta^*(x) \approx \Delta_m(x) = \lambda_m(x)\sigma^2$ where

$$(10)\quad \lambda_m(x) = \quad (1/2)\quad \frac{\alpha g g'[2V'' + V''' g]}{|r'' + \alpha(g')^2 V''|}.$$

Here the derivation depends again upon local approximations and a distribution with a relatively small variance. An intuitive explanation similar to Arrow's measures also exists for Δ_m, since $\partial^2/\partial D^2[\partial V(Dg(y))/\partial y] = g(y)g'(y)\{2V''(Dg(y) + Dg(y)V''\ '(Dg(y))\}$, which evaluated at $E(D) = 1$ is $gg'[2V'' + gV''']$. Scaling by the approximate expression for $|\partial^2 J/\partial y^2|$ yields $\lambda_m(x)$. Again, the sign of Δ_m will be consistent with the results of Proposition 3, Δ_m will be zero if $\partial/\partial y\ [V_d^*(Dg(y))]$ is linear in D (as required by Proposition 3), and $\Delta_m = 0$ of $\sigma^2 = 0$, a natural condition.

With multiplicative stochasticity, a quadratic value function for the deterministic model will not imply certainty equivalence, in general.

To use these measures, one must solve for the derivative of V_d^*, which is typically possible only for analytically tractable models. If one resorts to numerical calculation using recursion (3), the set of possible stock sizes is typically approximated by a finite set of discrete points, generating a nondifferentiable aproximate value function. In the following sections a polynomial approximation (derived via a least squares fit to the numerically generated value function V_d^*) guarantees the required differentiability and is used to infer the magnitude and direction of Δ^*. The methodology is not restricted to polynomial approximate functions but the investigation of alternative functional forms is left for future research.

Let λ denote λ_a or λ_m and Δ denote Δ_a or Δ_m, as appropriate for the model being considered. The heuristic measures $\lambda(x)$ use derivative information at the point x only whereas the real Δ^* will depend upon an expectation taken over states $x + D$

TABLE 3. Distributions for D used in general models.

No.		Probability mass function									
					Additive						
1	D_i	−4	−2	2	4						
	Prob_i	0.25	0.25	0.25	0.25						
2	D_i	−6	−4	−2	2	4	6				
	Prob_i	0.2	0.2	0.1	0.1	0.2	0.2				
3	D_i	−10	−8	−6	−4	−2	2	4	6	8	10
	Prob_i	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
4	D_i	−10	−8	−6	6	8	10				
	Prob_i	0.3	0.1	0.1	0.1	0.1	0.3				
5	D_i	−20	−15	−10	−5	−2	2	5	10	15	20
	Prob_i	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
6	D_i	−10	−8	−2	0	1	4	5			
	Prob_i	0.1	0.1	0.1	0.1	0.2	0.2	0.2			
7	D_i	−5	−4	−1	0	2	8	10			
	Prob_i	0.2	0.2	0.2	0.1	0.1	0.1	0.1			
					Multiplicative						
1	D_i	0.9	1.0	1.1							
	Prob_i	0.25	0.5	0.25							
2	D_i	0.7	0.9	1.0	1.1	1.3					
	Prob_i	0.2	0.2	0.2	0.2	0.2					
3	D_i	0.2	0.5	0.7	0.9	1.0	1.1	1.3	1.5	1.8	
	Prob_i	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.1	
4	D_i	0.1	0.25	0.5	0.7	1.0	1.6	2.0			
	Prob_i	0.1	0.2	0.1	0.1	0.1	0.2	0.2			
5	D_i	0.1	1.9								
	Prob_i	0.5	0.5								
6	D_i	0.71	0.76	0.94	1.0	1.12	1.47	1.59			
	Prob_i	0.2	0.2	0.2	0.1	0.1	0.1	0.1			
7	D_i	0.41	0.53	0.88	1.0	1.06	1.24	1.29			
	Prob_i	0.1	0.1	0.1	0.1	0.2	0.2	0.2			

or Dx as D varies over its range. Ideally, one would like to capture information from neighboring states in deriving one's estimate for Δ^*. This influence from neighboring states can result from curve fitting. The expectation is a smoothing operation, as is the operation of fitting a least squares curve. Consequently, one might expect lower order polynomial fits to give better results for distributions of high variance and/or skewness (letting the least squares smoothing be an approximation to taking the expectation) and higher order polynomials (which can be expected to better reproduce local behavior) to be better for tighter distributions. Choosing the appropriate order a priori is not possible, since only $E(D)$ is assumed known with precision. In the following sections a range of $\lambda(x)$ values is calculated from polynomial approximations to V_d^* of orders 3 through 6, the assumption being that the corresponding range of $\Delta(x)$ values can be expected to embrace the true $\Delta^*(x)$ no matter what the actual distribution of D.

Note that the λ measures depend only upon the solution to the deterministic model and can be used to divide the distribution functions for D into two sets, those for which stochasticity is not a major issue in prescribing policy and those for which no such claim can be made. In addition, since the measures are state specific, they can suggest those states most sensitive to stochastic shocks. If the fishery is not presently in a sensitive state, then the deterministic prescription can be used. Specifically, suppose that from a practical perspective managers will not be concerned about the effects of stochasticity if the deterministic and stochastic harvesting policies differ by k stock units or less. Let $\lambda_{\max}(x)$ denote the maximum $|\lambda(x)|$ over polynomial orders 3 through 6. Then if the fishery presently resides in state x, the managers will be unconcerned if $|\Delta^*(x)| \approx \lambda_{\max}(x)\sigma^2 \leq k$, or equivalently $\sigma^2 \leq k/\lambda_{\max}(x)$. Stochasticity is not a major issue in prescribing policy for distributions that satisfy this inequality. Again, if this class is sufficiently large (i.e. the set includes most of the plausible distributions for the fishery, as determined by management judgment or confidence intervals for the variance), then the deterministic model can be used to prescribe policy.

Those distributions for which stochasticity is not a practical issue in any state will be those for which $\sigma^2 \leq k/\lambda_{\max}$, where $\lambda_{\max}$ is the maximum over all states of $\lambda_{\max}(x)$. For example, in additive models if V_d^* is quadratic, $\lambda_{\max} = 0$ and the critical threshold is $\sigma^2 \leq \infty$, which includes all distribution functions.

The use of these measures in applications is demonstrated by example in the next section.

TABLE 4. Model Parameters for example applications.

A. Myopic model with lost repeatability

$\theta = 1 \qquad \alpha = 0.9$

$r(x, y) = 7.0(x-y) - 0.05 \log (x/y)$

$g(y) = \sum_{n=0}^{7} t_n y^n$

$t_0 = -2.05$	$t_4 = 1.97 \times 10^{-4}$
$t_1 = 1.57$	$t_5 = -3.44 \times 10^{-6}$
$t_2 = 3.17 \times 10^{-2}$	$t_6 = 2.8 \times 10^{-8}$
$t_3 = -5.06 \times 10^{-3}$	$t_7 = -8.65 \times 10^{-11}$

B. General Cobb–Douglas model

$\theta = 0.5 \qquad \alpha = 0.9$

$r(x, y) = \int_0^h p(h)dh - C(E)$

where $h = x - y$

$p(h) = 3 - 0.01h$

$E = (1-\theta)^{-1} [x^{1-\theta} - y^{1-\theta}]$

$$g(y) = \begin{cases} 0.1 + 0.1\, y^2 - 0.0017y^3 & y < 40 \\ 55.2 & y \geq 40 \end{cases}$$

TABLE 5. Δ^* and Δ results for myopic loss of repeatability model.

No. (σ^2)	y_s^*	Δ^*	$\Delta_a(x)$ or $\Delta_m(x)$ range
		Additive	
1 (10)	13	0	[0.1, 1.04]
2 (21.6)	14	1	[0.216, 2.24]
3 (44)	16	3	[0.44, 4.57]
4 (80)	17	4	[0.8, 8.32]
5 (150)	18	5	[1.5, 15.6]
6 (25.2)	15	2	[0.252, 2.62]
7 (25.2)	14	1	[0.252, 2.62]
		Multiplicative	
1 (0.005)	13	0	[−0.06, 0.075]
2 (0.04)	13	0	[−0.48, 0.6]
3 (0.198)	15	2	[−2.4, 2.98]
4 (0.4995)	15	2	[−6.0, 7.53]
5 (0.81)	13	0	[−9.72, 12.2]
6 (0.0874)	13	0	[−1.04, 1.31]
7 (0.0874)	15	2	[−1.04, 1.31]

Example Applications

In this section it is shown that lumped-parameter fishery models with constant or downward sloping linear demand curves, Cobb–Douglas production functions, and convex cost of effort will satisfy the isotonicity conditions required for the derivation of the λ measures in the previous section. Then, two specific examples are presented that demonstrate the use of these measures.

Consider a fishery system with the price of fish each time period a linear function of harvest, i.e. price $= p = a - bh$ where a and b are constants and $h =$ harvest $= x - y$. Then the total benefit to society for harvest h is $\int_0^h (a - bz)\, dz = ah - (b/2)h^2 = a(x-y) - (b/2)(x-y)^2$ which has isotone differences in x and y by direct inspection. Let $C(E)$ denote the cost of producing fishing effort level E. With a Cobb–Douglas production function (equation (8)) the effort necessary to harvest the resource from x to y in a single time period is

$$E = (1/q)(\log x - \log y) \qquad \text{if } \theta = 1$$
$$E = 1/(q(1-\theta))(x^{1-\theta} - y^{1-\theta}) \qquad \text{if } \theta \neq 1.$$

It can be verified that for any $\theta \geq 0$, $-C(E)$ will have isotone differences in x and y for any convex function C. Hence, $r(x,y) = a(x,y) - (b/2)(x-y)^2 - C(E)$ will have isotone differences in x and y for any convex C. This is the structure required in Proposition 3 and underlying the derivation of the λ measures.

The next two subsections contain example applications of Δ_a and Δ_m in two different models having these attributes. The "true" Δ^* in these examples was calculated via a successive approximations algorithm (see equation (3)) on a finite set of 100 discrete states 1,2,...,100 and the lowest state (state 1) absorbing, representing extinction. If $f(y,D)$ for a sample value of D left this set, then it was set equal to its closest point in the set, 1 or 100, essentially truncating the distribution of D near the extreme states. This is an approximation error inherent in any finite approximation and must be considered when interpreting the results. (Complete details are available from the author.) In the following two example applications, Δ was estimated from the solution to the deterministic model and the results compared with the numerically calculated Δ^* using a range of additive and multiplicative distributions for D. The distributions for D used are shown in Table 3.

Myopic Structure with Loss of Repeatability

The model class introduced above contains models with myopic structure ($b = 0$ and $C(\,)$ linear) as special cases. The example model in this section has this structure, with the parameter and function values shown in Table 4. The expected recruitment function used here is a polynomial representation of a function with depensatory behavior (cf. Clark 1976) at low population levels, a range (approximately $y = 3$ to 50) where $g(y)$ marginally outpaces y, and then a levelling off at $g(y) \approx 60$ for all $y > 50$. This nonstandard functional form was chosen deliberately because it represents a fishery that is marginal at best and is easily endangered by overfishing because of its depensatory behavior. Thus, it should be very sensitive to stochastic shocks. The deterministic model has a myopic optimum with $y_d^* = 13$, and $g(13) = 17$ ensures repeatability. The deterministic optimal policy is $\delta^*(x) = \min\{x,13\}$. From (4) we have $V_d^*(x) = 7x + 0.05 \cdot \log x + h \cdot (13)$ for $x > 13$, which is very nearly linear on that range. Since $V_d^{*\prime\prime}$ and $V_d^{*\prime\prime\prime} \approx 0$ for $x \geq 13$, we expect from Proposition 3 near certainty equivalence as long as $g(13) + D$ or $Dg(13)$ does not leave this linear region. This also follows from the observations concerning myopic models in section 3, since not leaving this region [13,100] implies repeatability. Hence for any additive distribution ensuring $D \geq -4$, or multiplicative distribution with $D \geq 0.76$, we can expect certainty equivalence. These ranges are rather restrictive, and there may be many plausible distributions that violate these limits. We must concern ourselves, then, with what happens when repeatability is lost. For this we will want to calculate λ_a or λ_m from the polynomial fits to V_d^*.

Additive stochasticity

For additive stochasticity, $\lambda_a(x)$ was positive for all x and all orders, implying that stochasticity will make us more conservative. How much more conservative will depend upon Δ_a. We will concentrate on stock levels in excess of 13, since it can be verified that for this model, λ_a is constant above this level. This

TABLE 6. General Cobb–Douglas model $\delta_d^*(x)$ and $\lambda(x)$ for selected states x.

State (x)	$\delta_d^*(x)$	Order 3	Order 4	Order 5	Order 6
		Additive stochasticity, $\lambda_a(x)$ by polynomial order			
10	10	0.0035	0.0084	0.0041	−0.2092
20	20	0.0053	0.0113	0.0092	0.0119
30	29	0.0104	0.0201	0.0234	0.2447
40	33	0.0130	0.0184	0.0261	0.5348
50	36	0.0114	0.0108	0.0162	0.0029
60	39	0.0029	0.0021	0.0032	−0.0010
70	45	0.0000	0.0000	0.0000	0.0000
80	51	0.0000	0.0000	0.0000	0.0000
90	57	0.0000	0.0000	0.0000	0.0000
		Multiplicative stochasticity, $\lambda_m(x)$ by polynomial order			
10	10	−3.3	−3.6	−3.7	−16.3
20	20	−6.6	−2.0	−3.8	−2.5
30	29	3.5	28.9	34.4	556.8
40	33	16.1	42.7	63.2	2294.7
50	36	19.9	31.0	48.7	59.2
60	39	5.9	6.7	10.5	3.9
70	45	0.0	0.0	0.0	0.0
80	51	0.0	0.0	0.0	0.0
90	57	0.0	0.0	0.0	0.0

constant value and the coefficient of determination R^2 for the polynomial fits of orders 3 through 6 to V_d^* are as follows:

Order	3	4	5	6
R^2	0.9904	0.9936	0.9959	0.9974
λ_a	0.011	0.027	0.053	0.104

Since $\Delta_a(x) = \lambda_a(x)\sigma^2$ for $x \geq 13$, we can solve for a threshold σ^2 below which we will expect near certainty equivalence. For example, suppose that we as policy makers are unconcerned if $|\Delta^*| \leq 2$, i.e. we will not expend additional resources to specify D if it will only result in a policy change of 2 units of stock or less on all of S. The above table implies that we need not be concerned if σ^2 is less than about 20, since then, $\lambda_a\sigma^2$ will be 2.08 or less.

To check this heuristic assessment, the dynamic program was solved with stochastic recruitment for each of the additive distributions for D in Table 3. In all cases the stochastic model had a base stock optimal policy, i.e. $\delta_s^*(x) = \min\{x, y_s^*\}$ with $y_s^* \geq 13$; hence, conservatism was verified. Table 5 shows Δ^* and the range of Δ_a values generated by polynomials of orders 3 through 6. $\Delta^* = y_s^* - 13$ is the numerically calculated difference in base stocks. The anticipated threshold of $\sigma^2 \leq 20$ is accurate for these additive models, and in all cases the range of Δ_a values generated by polynomial orders 3 through 6 embraces the calculated Δ^*.

It is interesting to note that for distributions that preserve repeatability, $\Delta^* \leq 0$ by Proposition 3. The empirical experiments under Myopic Models, however, suggest that we can expect $\Delta^* = 0$. As distributions get broader and repeatability is lost, we become more conservative, i.e. the observed $\Delta^* \geq 0$. This directional result is correctly anticipated by Δ_a.

Multiplicative stochasticity

The deterministic solution, i.e. $\partial_d^*(x) = \min\{x,13\}$, and the polynomial fits (and R^2 values) are the same in the multiplicative model as in the additive model ($f(y,E(d)) = g(y)$ in both). The $\lambda_m(x)$ values ranged through both positive and negative values, so that we are unsure of the directional effects of stochasticity in this case. Again, $\lambda_m(x)$ will be constant for $x \geq 13$. This constant λ_m is tabulated by polynomial order as follows:

Order	3	4	5	6
λ_m	−12.0	−7.27	0.4168	15.06

Here there is no clear indication of the direction of policy shift. If, again, we were unconcerned if $|\Delta^*| \leq 2$, then we could calculate from the above table a threshold σ^2 of about 0.13. To check this, the dynamic programs with multiplicative D and the distributions shown in Table 3 were solved numerically for δ_s^*. Again, a base stock policy was optimal in all stochastic models, and we can compare policies by the difference Δ^* in base stock levels. Δ^* and the range of $\Delta_m = \lambda_m\sigma^2$ values are shown in Table 5. $\Delta^* \geq 0$ in all cases, and the estimate of $\sigma^2 \leq 0.13$ implying $|\Delta^*| \leq 2$ was accurate for these distributions. In all cases except distribution 7 (skewed with a longer lower tail) the range of Δ_m values generated embraced the numerically calculated Δ^*. For distribution 1 and 2, the range of Δ_m values strongly predicts the observed certainty equivalence. Note that these are not modest stochastic shocks, e.g. distribution 2 allows for $g(y)$ to be stochastically adjusted by ±30%. For the largest variance distributions the range of Δ_m values was broader than necessary, but still embraced Δ^*. Note that these reflect dramatic stochasticity, e.g. distribution 5 will yield a 50/50 chance of getting 10 or 190% of $g(y)$ and nothing in between.

In these examples the heuristic measure $\lambda\sigma^2$ was most accurate in predicting Δ^* for low variance distributions. This is to be expected, since the derivation of the measures uses a Taylor series approximation that is most accurate in the neighborhood of δ_d^*. Intuitively, the λ measures may be interpreted as the marginal rate of change of the optimal policy for marginal increases in variance, evaluated at $\sigma^2 = 0$ (the deterministic model). For higher variance distributions the interval generated by the range of polynomials was broader than necessary. This is also to be expected. The heuristic Δ range is intended to suggest the true Δ^* range for any distribution with the specified mean and variance, which can include distributions of different skewness and different Δ^* values. Hence the range of Δ values must be broad enough to reflect the range of Δ^* values that can result. For example, the Δ_a range is conservative for additive distribution 7 but not so for 6 (and vice versa for multiplicative distributions 6 and 7). Distributions 6 and 7 have identical means and variances, but differ in skewness. This indicates that these measures are useful as conservative estimates, i.e. if certainty equivalence is indicated, then that is what one can expect, but if a broad range of Δ values is generated, then it indicates that one can say little with only the deterministic solution, and more information is required concerning D. Alternatively, the upper bound, $\sigma_{\max}(x) = k/\Delta_{\max}(x)$ on σ^2 to anticipate $|\Delta^*(x)| \leq k$, can be expected to be conservative in that for distributions with variances below this bound, one can expect Δ^* to be less than k, but this may hold as well for higher variance distributions. Hence, $\sigma_{\max}$ is an efficiently calculated measure of how much stochasticity we can inject into the model before dramatic policy shifts may be necessary.

If confidence limits are available concerning σ^2, then the equation $\Delta^*(x) \approx \lambda(x)\sigma^2$ can be used directly to estimate worst case policy shifts due to stochasticity.

TABLE 7. Stochastic model results of the general Cobb–Douglas model additive and multiplicative distributions.

			Additive		Multiplicative	
No.	State (x)	$\delta^*_d(x)$	$\Delta^*(x)$	$\Delta_a(x)$ range	$\Delta^*(x)$	$\Delta_m(x)$ range
1	10	10	0	[−2.1, 0.084]	0	[−0.081, −0.016]
	20	20	0	[0.053, 0.119]	0	[−0.033, −0.01]
	30	29	0	[0.104, 2.45]	0	[0.018, 2.78]
	40	33	0	[0.13, 5.35]	0	[0.081, 11.47]
	50	36	0	[0.0292, 0.162]	0	[0.1, 0.296]
	60	39	0	[−0.01, 0.032]	0	[0.019, 0.052]
	70	45	0	[0, 0]	0	[0, 0]
	80	51	0	[0, 0]	0	[0, 0]
	90	57	0	[0, 0]	0	[0, 0]
3	10	10	0	[−9.2, 0.37]	0	[−3.23, −0.65]
	20	20	0	[0.233, 0.523]	0	[−1.3, −0.39]
	30	29	1	[0.458, 10.8]	1	[0.7, 110.2]
	40	33	0	[0.572, 23.5]	0	[3.19, 454.4]
	50	36	0	[0.128, 0.713]	1	[3.94, 11.71]
	60	39	0	[−0.044, 0.1408]	0	[0.76, 2.08]
	70	45	0	[0, 0]	0	[0, 0]
	80	51	0	[0, 0]	0	[0, 0]
	90	57	0	[0, 0]	0	[0, 0]
6	10	10	0	[−5.27, 0.21]	0	[−1.43, −0.29]
	20	20	0	[0.133, 0.3]	0	[−0.577, −0.172]
	30	29	0	[0.262, 6.2]	0	[0.31, 48.66]
	40	33	0	[0.328, 13.48]	0	[1.41, 200.6]
	50	36	0	[0.74, 0.41]	0	[1.74, 5.17]
	60	39	0	[−0.025, 0.08]	0	[0.337, 0.916]
	70	45	0	[0, 0]	0	[0, 0]
	80	51	0	[0, 0]	0	[0, 0]
	90	57	0	[0, 0]	0	[0, 0]
7	10	10	0	[−5.27, 0.21]	0	[−1.43, −0.287]
	20	20	0	[0.133, 0.31]	0	[−0.578, −0.172]
	30	29	1	[0.262, 6.2]	1	[0.309, 48.66]
	40	33	0	[0.328, 13.48]	0	[1.41, 200.6]
	50	36	0	[0.074, 0.41]	0	[1.74, 5.17]
	60	39	0	[−0.25, 0.08]	0	[0.337, 0.916]
	70	45	0	[0, 0]	0	[0, 0]
	80	51	0	[0, 0]	0	[0, 0]
	90	57	0	[0, 0]	0	[0, 0]

A More General Cobb–Douglas Model

In this section the heuristic measures are used with a Cobb–Douglas model with downward sloping demand curve and increasing marginal cost of effort. The model details are displayed in Table 4. The expected recruitment, $g(y)$, exhibits depensatory behavior for y less than about 30 and $g(y) < y$ for $y < 11$. The deterministic model was solved numerically and the heuristic measures $\Delta_a(x)$ and $\Delta_m(x)$ used to anticipate the direction and magnitude of the effects of stochasticity. Then, for comparison, stochastic models were solved numerically for each of the distributions introduced above. Additive and multiplicative models are discussed in turn.

Additive stochasticity

The optimal deterministic policy and $\lambda_a(x)$ are tabulated for selected states in Table 6. Note that unlike the model in the previous section, a constant escapement policy is not optimal here and λ_a will vary with state. This measure indicates that we should be concerned about the effects of stochasticity around states 10, 30, and 40. Specifically, if again we are unconcerned if $|\Delta^*| \leq 2$, then λ_a suggests $\sigma^2 \leq 3.7$. If we consider all states except those around 10, 30, and 40, $\sigma^2 \leq 76.6$ will suffice. Our prior judgement, then, would be that we can inject substantial additive stochasticity and still not dramatically perturb the optimal policy in all states except those around 10 to 40. In these sensitive states, we would need more information regarding D to say anything substantive.

The numerically calculated Δ^* and the range of Δ_a values predicted over all polynomial orders are shown in Table 7 for selected states and distribution numbers 1, 3, 6, and 7. The results from distributions 2, 4, and 5 were similar. The $\Delta_a(x)$ measure generally brackets, or nearly so, the actual $\Delta^*(x)$ values, and the only departures from certainty equivalence occur in state $x = 30$, correctly targeted as a sensitive state by λ_a. However, dramatic departures from δ_d^* did not materialize, so the broad ranges of Δ_a in states 10, 30, and 40 are overly conservative. By contrast the tight Δ_a ranges outside this sensitive range allow us to predict near certainty equivalence with confidence.

Multiplicative stochasticity

The optimal deterministic policy and $\lambda_m(x)$ are tabulated for the selected states in Table 6. The directional indications are that in the face of stochasticity, we will be more liberal in states 10 to 20 and conservative for stock levels exceeding 20. The magnitudes indicate that, directional effects aside, we will have

near certainty equivalence for low or moderate variance distributions in all other states. Indeed, one can verify that for multiplicative distributions with variances less than 0.12, we would expect the policy shift to be less than or equal to two stock units in all states except 30 to 50. In states 30 to 50 the measures indicate a possibly dramatic conservative shift in the stochastic policy, but as suggested above, broad ranges are to be interpreted as calling for more precise information concerning the distribution of D.

The liberal indications in states 10 and 20 are interesting, and difficult to interpret. The effect may be real (proportional stochasticity can easily doom a fishery with a large $g(y) \leq y$ range, fostering a cavalier attitude that prescribes harvests as if there were no tomorrow) or apparent (the polynomial model has spurious oscillations that do not properly represent the system). The absolute values are, however, small, and we expect certainty equivalence for low variance distributions.

Table 7 presents Δ^* and the Δ_m range for the selected states and distributions. The only states to waver from certainty equivalence in the numerical solutions are states 30 and 50, which are in the sensitive range targeted by λ_m. The policy shift, however, is only one stock unit, and not the dramatic response that Δ_m indicates is possible. The Δ_m range predicted from the deterministic model embraced, or very nearly so, the numerically calculated Δ^* values in most cases, but there were exceptions. The predicted range missed the numerically calculated Δ^* by over three stock units at $x = 40$ with distribution 3.

In summary, less can be said a priori in this example, but what can be said is confirmed by the numerical results. Specifically, using only λ_m, we can predict near certainty equivalence for distributions with $\sigma^2 \leq 0.12$ for all states except 30 to 50. For states 30 to 50, we can expect a possibly dramatic conservative shift, but we need more specific information regarding the distribution of D to say anything with confidence.

Conclusions

This paper assumes that one starts with a known deterministic, lumped-parameter fisheries model, and is interested in determining how much stochasticity can be introduced into the stock dynamics before the policy prescription changes. Stochasticity is expected to have little effect in models with myopic structure and repeatable solutions. For more general models, it is assumed that the deterministic model is solved numerically for the optimal value function using an approximate model with a finite number of population or biomass levels. Then, a polynomial is fit to this approximate value function using any standard curve fitting technique. The change in the optimal policy between the deterministic and the stochastic model at stock level x is then approximated by $\lambda\sigma^2$, where λ can be calculated directly from the deterministic problem data and the approximate value function and σ^2 is the variance of the random parameter introduced into the model. Both additive and multiplicative randomness can be considered.

The predictions will depend upon the order of the polynomial used to approximate the value function, corresponding to different levels of smoothing imposed upon the numerical results. The appropriate polynomial order to use is not known, a priori. However, by recalculating the results for each of polynomial orders 3, 4, 5, and 6, a range of predictions is generated that can be expected to embrace the true magnitude of the policy shift. Thus, the measures can be used to identify those states that will be most sensitive to stochastic shocks and to bound the policy differences between the deterministic and stochastic models.

The λ measures for additive models depend upon the third-order behavior of the optimal value function in the deterministic model. This means that if a quadratic function can closely approximate the value function for the deterministic fishery model, then additive stochastic shocks will not affect policy. This is consistent with some known results in models with linear dynamics, quadratic reward functions, and additive stochasticity. For models that do not guarantee quadratic value functions, λ uses the nonzero third-order behavior to anticipate the departure from certainty equivalence.

The measures for multiplicative stochasticity depend upon both the second- and third-order behavior of the optimal value function in the deterministic model. Thus, for these models, quadratic value functions are not expected to exhibit certainty equivalence, in general.

The λ measures are state dependent and can be used to identify those states that are most sensitive to stochastic shocks. For example, it is plausible that the deterministic value function will be nearly quadratic at robust stock levels but depart from this behavior at low stock levels, where extinction is a possibility. In this case, for additive stochasticity the measures would indicate certainty equivalence when the stock is healthy but an altered harvesting policy when it is endangered. This is consistent with intuition, and the numerical measures can help identify the "healthy," or certainty equivalent, stock levels.

For multiplicative stochasticity, linear behavior is required for certainty equivalence. A model with myopic structure can exhibit this behavior at healthy stock levels. Again, the measures can help identify this healthy region.

In summary, the solution to a deterministic fishery harvesting problem contains some, but not all, information regarding how the optimal policy will respond to stochastic shocks. In this paper, some rigorous and heuristic results have been presented that can summarize the information available in the deterministic solution and indicate where one might wish to focus additional information gathering activities.

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Appendix A: $\beta(y)$ for Additive Stochasticity in Myopic Models

For additive stochasticity in myopic models:

$$\beta(y) = g'(y)[c(g(y)) - Ec(g(y)+d)].$$

Expanding $c(x) = k/x^\theta$ in second-order Taylor series about $g(y)$ yields

$$c(g(y) + d) \approx k \left[\frac{1}{g(y)^\theta} - \frac{\theta d}{g(y)^{1+\theta}} + \frac{\theta(1+\theta)d^2}{2g(y)^{\theta+2}} \right]$$

and since $E(d) = 0$, we have

$$Ec(g(y)+d) \approx k \left[\frac{1}{g(y)^\theta} - 0 + \frac{\theta(1+\theta)\sigma^2}{2g(y)^{\theta+2}} \right].$$

Hence

$$\beta(y) \approx -g'(y)k \frac{\theta(1+\theta)\sigma^2}{2g(y)^{\theta+2}}.$$

where σ^2 is the variance of d. Thus, since $\Gamma_s'(y) = \Gamma_d'(y) + \alpha\beta(y)$, the $g(y)^{\theta+2}$ in the denominator of the last $(\alpha\beta(y))$ term suggests that this term will have relatively little effect on the total expression for all but the most modest values of y, i.e. $\Gamma_s'(y) \approx \Gamma_d'(y)$ and we might expect near certainty equivalence.

Appendix B: $\beta(y)$ for Multiplicative Stochasticity in Myopic Models with $\theta \in [0,2]$

Expanding $c(dg(y))$ in a second-order Taylor series about $g(y)$ yields

$$c(dg(y)) = k \left[\frac{1}{g(y)^\theta} - \frac{\theta}{g(y)^{1+\theta}} (dg(y) - g(y)) \right] + \frac{\theta(1+\theta)}{2g(y)^{\theta+2}} (d^2 g(y)^2 - 2dg(y)^2 + g(y)^2).$$

Thus

$$dc(dg(y)) \approx \frac{k}{g(y)^\theta} \left[d - \theta d^2 + \theta d + \frac{\theta(1+\theta)}{2}(d^3 - 2d^2 + d) \right]$$

and since $E(d) = 1$, implying $E(d^2) = \sigma^2 + 1$:

$$E(dc(dg(y))) \approx \frac{k}{g(y)^\theta} \left[1 - \theta\sigma^2 + \frac{\theta(1+\theta)}{2}(E(d^3) - 2\sigma^2 - 1) \right].$$

Thus

$$\beta(y) = g'(y)(c(g(y)) - Ec(dg(y))d) \approx \frac{\theta k g'(y)}{g(y)^\theta} \left[\sigma^2 - \frac{1+\theta}{2}(E(d^3) - 2\sigma^2 - 1) \right].$$

To bound this, let ξ = the bracketed term on the right-hand side. We have from the Schwarz inequality $[E(d_2)]^2 = E[(d^{3/2})(d^{1/2})]^2 \leq E(d^3)E(d)$, so $E(d^3) \geq (\sigma^2+1)^2 \geq \sigma^2+1$, which will imply $\xi \leq \sigma^2[(3+\theta)/2]$.

We know from Proposition 3 that if $\theta \geq 1$, we have $\beta(y) \leq 0$, so we can bound $\xi \leq 0$ in this case. If $\theta \leq 1$, then $\xi \leq 2\sigma^2$; hence, for all $\theta \geq 0$ we have $\xi \leq 2\sigma^2$.

Let $d \leq t$ with probability one. Then $E(d^3) \leq t\,E(d^2) = t(\sigma^2 + 1)$, and $\xi \geq [\sigma^2 - (1+\theta)/2\,((t-2)\,\sigma^2 + t - 1)]$. If $t=2$, then $\xi \geq \sigma^2 - (1+\theta)/2$. For $\theta \in [0,2]$ we have $\xi \geq \sigma^2 - 3/2 \geq - \geq 3/2$.

Also, if $t = 2$, then $d - E(d) = d - 1 \leq 1$ and $\sigma^2 \leq 1$, so

$$\left(-\frac{3}{2} \right) \frac{\theta k g'(y)}{g(y)^\theta} \leq \beta(y) \leq (2) \frac{\theta k g'(y)}{g(y)^\theta}.$$

For θ close to zero, $\Gamma_s'(y) \approx \Gamma_d'(y)$; for $\theta = 1$, these derivatives are exactly equal from Proposition 2, and as θ increases from 1 the influence of the β term diminishes due to the $g(y)^\theta$ in the denominator.

Appendix C: Heuristic Derivation of $\lambda_a(x)$

The theoretical underpinnings for Proposition 3 guarantee that if V_d^* is used as an initial value function in the stochastic recursion, then convexity (concavity) of the specified derivative will ensure that the approximate policies generated each iteration will be consistently increasing (decreasing) from δ_d^*. Thus, for any x the absolute difference between $\delta_d^*(x)$ and the maximizing argument in $J(x,y,V_d^*)$ bounds the optimal policy change $\Delta^*(x)$. Since empirically the policy changes tend to be most dramatic in the early iterations of such an algorithm, the above difference may be a used as a heuristic measure for Δ^*.

For notational simplicity, let V denote the deterministic optimal value function, V_d^*. Let y_d be an optimal action at x and let $r = r(x,y_d)$, $r' = \partial r/\partial y(x,y_d)$, $r'' = \partial^2 r/dy^2(x,y_d))$, $g = g(y_d)$, $g' = \partial g/\partial y(y_d)$, and $V^{(n)} = \partial^n V/\partial x^n(g(y_d))$ then for an interior solution $r' + \alpha V' g' = 0$. Using V as the approximate value function in the stochastic problem, we seek a y that maximizes $J(x,y,V)$ (see equation (2)). Approximating r by a second-order Taylor series in y about (x,y_d), g by a first-order series about y_d, and V with a third-order series about $g(y_d)$, we have

$$\begin{aligned} J(x,y,d) \approx r &+ r'(y-y_d) + (1/2)\, r''(y-y_d)^2 \\ &+ \alpha E[V + V'(g + g'(y-y_d) - g + d) \\ &+ (1/2)V''(g + g'(y-y_d) - g + d)^2 \\ &+ (1/6)V'''(g + g(y-y_d) - g + d)^3]. \end{aligned}$$

Setting $\partial J/\partial_y = 0$ and noting $E(d) = 0$, $E(d^2) = \sigma^2$, and $r' + \alpha V' g' = 0$ yields a quadratic equation $a\Delta^2 + b\Delta + c = 0$ where $\Delta = y_s - y_d$ and $a = (\beta/2)V'''(g')^3$, $b = r'' + \beta V''(g')^2$, and $c = (\beta/2)V''' g'\sigma^2$, implying $\Delta = (-b \pm \sqrt{b^2 - 4ac})/(2a)$.

Approximating the square root function by first-order Taylor series yields $\sqrt{b^2 - 4ac} \approx b - 2ac/b$ which implies $\Delta \approx -c/b$ or $-b/a + c/b$. Intuitively we choose $-c/b$ so that $\Delta \to 0$ as $\sigma^2 \to 0$, so

$$\Delta \approx -\frac{1}{2} \frac{\alpha V''' g'}{r'' + \alpha V''(g')^2} \sigma^2.$$

Appendix D: Heuristic Derivation of $\lambda_m(x)$

Expanding $J(x,y,V)$ about $y_d = \delta^*_d(x)$ as in Appendix C yields

$$J \approx r + r'(y-y_d) + (1/2)\, r''(y,y_d)^2 + \alpha E[V + V'(dg + dg'\,(y-y_d) - g) + (1/2)V''(dg + dg'(y-y_d) - g)^2 + (1/6)V'''(dg + dg'(y-y_d) - g)^3].$$

Setting $\partial J/\partial y = 0$ and noting $E(d) = 1$, $E(d^2) = \sigma^2 + 1$, and $r' + \alpha V' g' = 0$ yields a quadratic equation as in Appendix C with $a = (1/2)\alpha V'''(g')^3\, E(d^3)$, $b = r'' + \alpha V''(g')^2 E(d^2) + \alpha V''' g(g')^2\, [E(d^3) - E(d^2)]$, and $c = \alpha V'' g g' E(d^2) - \alpha V'' g g' + (1/2)\alpha V''' g' g^2 [E(d^3) - 2E(d^2) + 1]$.

Approximating d^3 in Taylor series about 1, $d^3 \approx 1 + 3(d-1) + 3(d-1)^2$, so $E(d^3) \approx 1 + 3\sigma^2$. Using this expression and approximating $\Delta = y_s - y_d$ by $-c/b$, as in Appendix C, yields

$$\Delta \approx -\frac{1}{2}\, \frac{\alpha g g' [2V'' + V''' g]\sigma^2}{r'' + \alpha V''(g')^2 \quad + \alpha (g')^2 (V'' + 2V''' g)\sigma^2}.$$

For σ^2 sufficiently small (note for even broad multiplicative distributions, say $0 \leq d \leq 2$, we will have $\sigma^2 \leq 1$), this approximately equals

$$-\frac{1}{2}\, \frac{\alpha g g' [2V'' + V''' g]}{r'' + \alpha V''(g')^2}\, \sigma^2.$$

Substrate Preferences of Brown Trout Fry (*Salmo trutta*) in Artificial Stream Channels

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Brown trout fry (*Salmo trutta*) of two sizes (43 and 32 mm mean total length) preferred the coarsest gravel when allowed to choose between three sizes (8–16, 20–30, and 50–70 mm) at two temperatures (12.9–18.1 and 6.0–6.9°C) in artificial stream channels. Fry hid more in the substrate in daytime than at night and in daytime also hid more at low temperatures than at high temperatures. Increasing the average water velocity from 4 to 14 $cm \cdot s^{-1}$ displaced the 43-mm fry slightly downstream at night. The 32-mm fry showed a weaker preference for the coarse substrate and, in general, had less pronounced diurnal substrate preferences.

Des alevins de truite brune (*Salmo trutta*) de deux tailles (43 et 32 mm de longueur totale moyenne) préféraient le gravier plus grossier lorsqu'ils pouvaient choisir entre trois granulométries différentes (8–16, 20–30 et 50–70 mm) à deux températures (12,9–18,1°C et 6,0–6,9°C) dans des chenaux de cours d'eau artificiel. Ils se dissimulaient davantage dans le substrat pendant le jour que pendant la nuit, et pendant le jour ils se dissimulaient davantage à basse température qu'à température élevée. Les alevins de 43 mm étaient légèrement déplacés en aval la nuit lorsque la vitesse moyenne de l'eau passait de 4 à 14 $cm \cdot s^{-1}$. Les alevins de 32 mm présentaient une préférence moins marquée pour le substrat grossier, et en général leurs préférences diurnes du substrat étaient moins marquées.

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Substrate is an important factor determining habitat suitability for trout in streams. Brown trout (*Salmo trutta*) have specific preferences for the size of spawning substrate, normally that of gravel (Frost and Brown 1967) with diameter in the range 10–20 mm (Reiser and Wesche 1977; Shirvell and Dungey 1983). Trout stream manipulations to enhance substrate have focused on spawning substrate and substrate preferred by adult brown trout, while the substrate preferences of brown trout fry have not usually been considered separately. The objective of the present study was to define substrate size preferred by different sizes of underyearling brown trout in artificial stream channels.

Selection of particular substrate sizes by brown trout in streams has been demonstrated (Bohlin 1977; Karlstrøm 1977; Baglinière and Champigneulle 1982). Addition of large rubble or rock substrate material has reduced downstream movement of steelhead trout (*Salmo gairdneri*) as water temperature declined at onset of winter (Chapman and Bjornn 1969; Bjornn 1971), which may indicate an increased habitat suitability for overwintering. A similar effect of added substrate material may be responsible for an increase in average population densities of juvenile Atlantic salmon (*Salmo salar*) in the Big Tricadie River, New Brunswick (Gilbert 1978). Suitable substrate seems to be important as shelter for trout and salmon at low temperatures (Chapman and Bjornn 1969; Bjornn 1971; Bustard and Narver 1975a, 1975b). Rimmer et al. (1984) demonstrated that large stones (>20 cm) provided low-temperature habitats for juvenile Atlantic salmon. These authors suggested that high autumnal immigration of juvenile Atlantic salmon into sections of two small Miramichi River tributaries may possibly be due to a lack of suitable substrate upstream (Randall and Paim 1982). Similarly, Hillman et al. (1987) demonstrated that addition of cobble substrate in a stream section increased the winter holding capacity of the stream section for juvenile chinook salmon (*Oncorhynchus tshawytscha*). My working hypothesis was that young brown trout might also show a stronger preference for hiding in interstices among stones at lower temperatures.

Water velocity also influences habitat choice by brown trout (Lewis 1969; Bohlin 1977; Karlstrøm 1977; Binns and Eiserman 1979; Baglinière and Champigneulle 1982; Kennedy and Strange 1982; Shirvell and Dungey 1983). There is a close relationship between water velocity and substrate, i.e. water velocity in part determines substrate character. The two factors may therefore be difficult to evaluate separately in preference studies in the natural habitat.

Stream-dwelling brown trout spend most of their time near the streambed rather than in midwater or close to the surface (Jenkins 1969; Shirvell and Dungey 1983; Bachman 1984; Cunjak and Power 1986). Stream velocity diminishes near the bed, and it is therefore energy-saving to maintain a position there (Bachman 1984; Fausch 1984). Consequently, it seemed reasonable to test the hypothesis that young brown trout would display stronger preferences for sheltering in substrate at high than at low water velocity.

There is some evidence that brown trout tend to be inactive at night (Lindroth 1955; Swift 1962, 1964), and Kalleberg (1958), studying fry of brown trout and Atlantic salmon in a stream aquarium, reported that "at least some fry...night after night made use of the same sleeping places in fissures between

stones." Several salmonid species apparently exhibit diurnal–nocturnal shifts in habitat positions (Chapman and Bjornn 1969), moving to positions providing more cover at daylight. However, studies on nighttime habitat use and preferences by salmonids are few.

This paper presents experimental results for substrate size preferences of two different size-classes of underyearling brown trout. Preferences were tested with regard to time of day or night (light intensity), water temperatures, and water velocities.

Methods

The experiments were performed at the Norwegian Water Research Institute's research station, situated at the Oset water treatment plant, the main water supply for the city of Oslo. Four similar stream channels served as controlled-flow experiment channels. The two low-temperature channels were supplied with hypolimnion water from nearby Lake Maridalsvannet. Water temperature ranged from 6.0 to 6.9°C during the test period. The high-temperature channels were supplied with epilimnion water. Water temperature ranged from 12.9 to 18.1°C. The oxygen level in the water was at all times close to saturation.

The channels, made of off-white fibreglass-reinforced polyester with a rectangular cross-section shape, were 15 m long, 20 cm wide, and 15 cm high and had adjustable overflow at the end of the channels. Water depth was kept at 12 cm. Water depth and velocities in the various channels, measured with a Schiltknecht Micro Mini water velocity meter, were nearly identical. Baffles in the channel inlets dispersed flow evenly. Each channel was closed with screens of 2-mm mesh at each end.

The approach was to offer underyearling brown trout three different substrate sizes in each channel: 8–16, 20–30, and 50–70 mm. Judging from previous research (Reiser and Wesche 1977; Shirvell and Dungey 1983), a particle size in the range 10–20 mm was considered to be the optimal spawning substrate size for brown trout. This would therefore be the size usually encountered by brown trout fry after emerging from the redds. The experimental substrate sizes were chosen to cover the lower and upper limits of what is considered to be the optimal spawning substrate size. A substrate size considerably larger was also chosen on the hypothesis that this size would be preferred because it provided ample interstices to seek shelter in.

Each channel contained three patches of each substrate size, i.e. nine patches, randomly distributed along the channel. In that way, effects of features known to influence position choice other than substrate size were randomized. Each patch was a 70 × 20 cm rectangle and approximately 6 cm thick. The patches were systematically spaced along the channels with a distance of 90 cm between each.

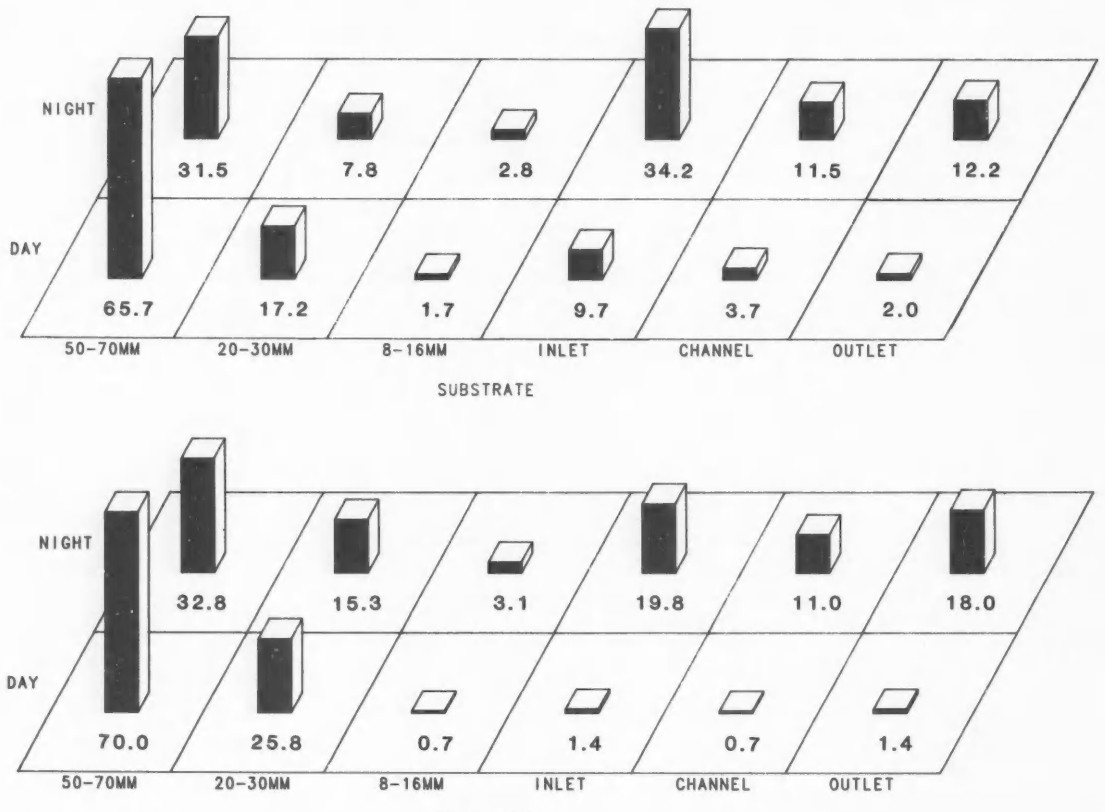

FIG. 1. Day and night frequencies (percent) of observations of 43-mm brown trout in the different substrate segments (sizes indicated) and segments without substrate (inlet, outlet, and channel) in stream channels at an average water velocity of 4 $cm \cdot s^{-1}$ and temperatures of 12.9–18.1°C (upper) and 6.0–6.9°C (lower). Data are pooled.

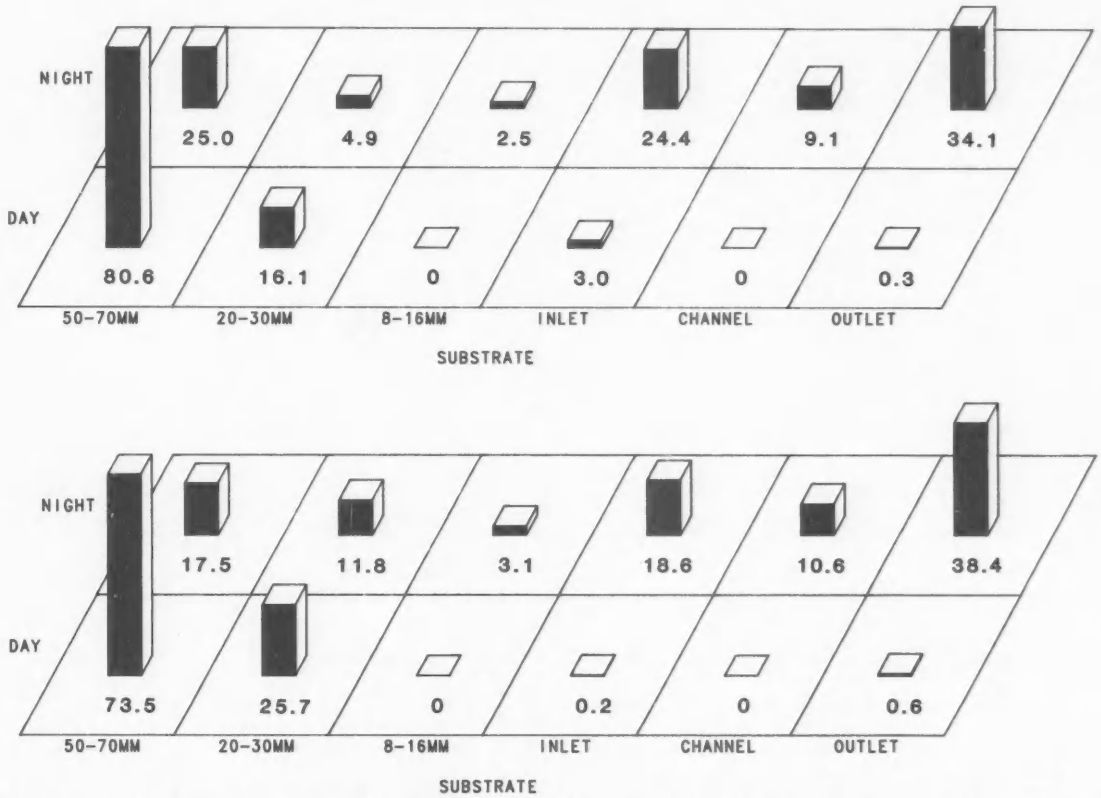

FIG. 2. Day and night frequencies (percent) of observations of 43-mm brown trout in the different substrate segments (sizes indicated) and segments without substrate (inlet, outlet, and channel) in stream channels at an average water velocity of 14 cm·s^{-1} and temperatures of 12.9–18.1°C (upper) and 6.0–6.9°C (lower). Data are pooled.

The fry were of two different length groups, averaging 32 (SD ±3) and 43 (SD ±3) mm total length. A total of 800 brown trout, 400 in each length group, were used in the experiment. Fish were supplied from the neighbouring NIVA Fish Hatchery, which used the same water supply as that in the experiments. In tests of 5-d duration, fish from one size group were introduced evenly into the channels. Observations started on the second day. First, fish from the larger length group were tested for substrate preferences at high and low temperatures at an average water velocity of 4 cm·s^{-1}. The same fish were then tested for substrate preferences at an increased water velocity of 14 cm·s^{-1}. Lastly, fish from the smaller length group were tested for substrate preferences at high and low temperatures at an average water velocity of 14 cm·s^{-1}.

The position of each fish was noted every 8 h during day and night and under natural lighting conditions, i.e. 2 day and 1 night countings per day. To avoid frightening fish during counting, only one trained observer was used. All fish in the 90-cm spaces between patches were easily visible and were counted first from one viewpoint above and behind the channels. Afterwards the observer moved upstream along the channels, inserting screens of 2-mm mesh at both ends of each patch of substrate. As the channels were raised about 115 cm above the ground, the crouched observer could move along them without being visible to the fish. Fish in each patch were counted as thoroughly as possible by carefully sorting through the substrate and turning the stones. Fish in the 90-cm spaces between patches which were frightened by the observer and escaped into the nearest substrate patch were subtracted from the count. Fish hiding upon or in the substrate only rarely showed any fright reaction. If fish were frightened onto a different patch than they were originally using, and it could not be decided from which patch they came, they were not counted. At night the same procedure was followed, using a flashlight. Fish were not fed during the experiments.

To check the efficiency of the observer, at the end of each test the fish were first counted in the usual manner. Then all the substrate in a closed patch was removed and the fish were counted once more. Two-way ANOVA without replication and likelihood-ratio tests (G-tests) were used to test the significance of substrate preferences.

Results

On average, 75% of the total number of fish were detected by the counting method used. The method showed no significant bias with regard to the number of fish counted in the different types of stream channel segments (ANOVA, number of fish observations corrected for the 25% underestimate in numbers as found by check, $P > 0.05$).

Highly significant preferences ($P < 0.05$) for different types of substrate occurred in all tests, and the preferences were con-

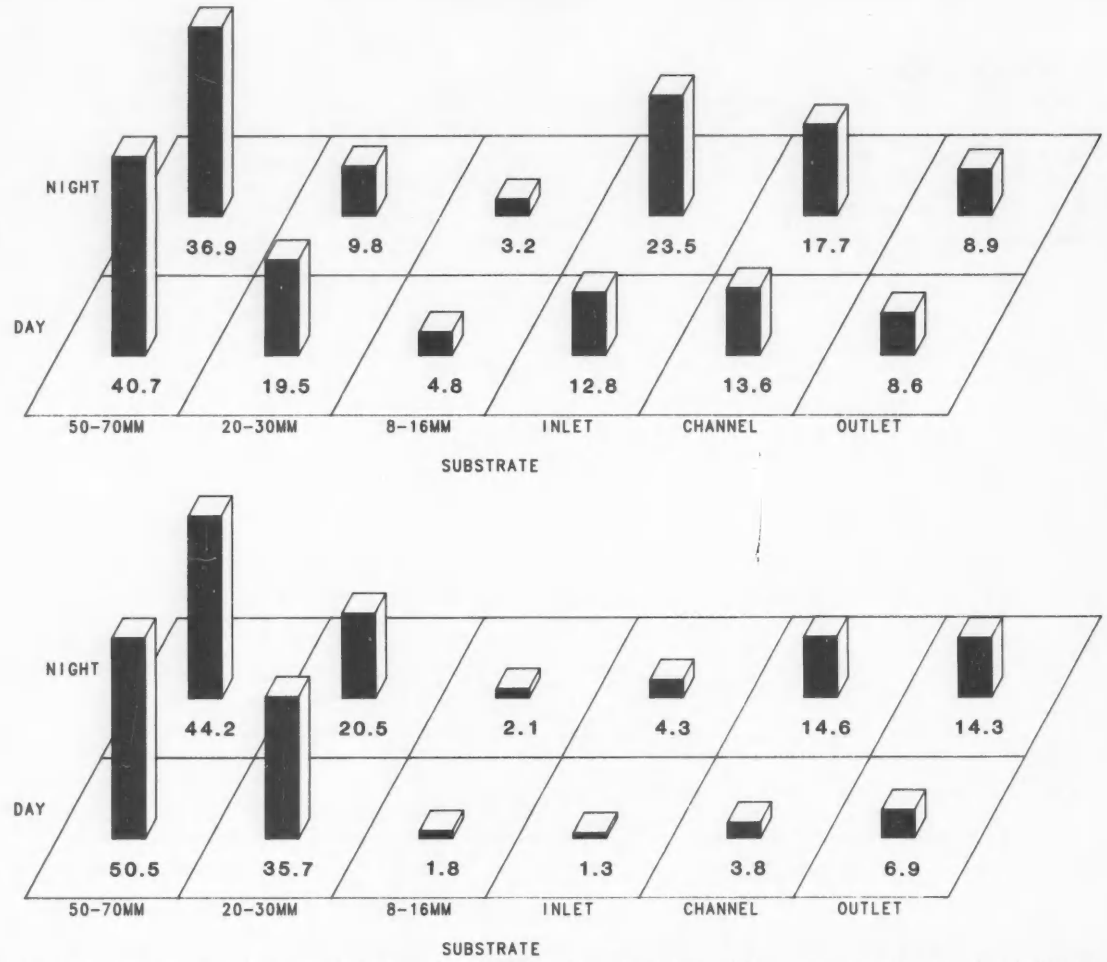

FIG. 3. Day and night frequencies (percent) of observations of 32-mm brown trout in the different substrate segments (sizes indicated) and segments without substrate (inlet, outlet, and channel) in stream channels at an average water velocity of 14 $cm \cdot s^{-1}$ and temperatures of 12.9–18.1°C (upper) and 6.0–6.9°C (lower). Data are pooled.

sistent throughout the experimental period (ANOVA, $P > 0.05$). Fry preferred the coarsest gravel substrate (Fig. 1–3).

The strength of the preference, however, was affected by fry size, water temperature, daytime or nighttime, and to some degree also by the water velocities. During daytime the larger 43-mm fry displayed strongest preference for the coarsest substrate (Fig. 1 and 2), 50–70 mm (G-tests, $P < 0.05$). On average, only 5.8% of the 43-mm fry were observed outside the gravel substrate patches in daylight; of the remaining 94.2% observed in gravel patches, 72.5% were observed in the coarsest substrate (50–70 mm) and only 0.6% in the finest substrate (8–16 mm).

The larger fry had significantly different distributions within the channels during day and night (G-tests, $P < 0.05$), in that considerably more fish were observed outside the gravel substrate patches at night (on average 60.5%). The inlets and outlets, which had no substrate, had an attracting effect on these fry (Fig. 1 and 2). Of the fraction of fry observed within substrate patches at night (on average 39.5%), a significant preference for the coarsest substrate was again found (G-tests, $P < 0.05$). The occurrence of so many fish outside the substrate patches at night made inferences as to the nighttime substrate preferences of the 43-mm fry difficult.

A significant difference between high and low water temperatures was also observed for 43-mm fry (G-tests, $P < 0.05$). More of these fry hid in the substrate in daytime at low temperatures, but no such effect was observed at night.

Increasing the water velocity from 4 to 14 $cm \cdot s^{-1}$ did not significantly affect the daytime substrate preferences of the larger 43-mm fry at either temperature (G-tests, $P > 0.5$). However, at 14 $cm \cdot s^{-1}$ at night, fewer large fry were observed at the inlet and in the sections in between substrate patches and more were observed at the outlet than at 4 $cm \cdot s^{-1}$ at both temperatures (G-tests, $P < 0.05$).

The smaller 32-mm fry also had significant preferences for the coarsest gravel substrate during both day and night and at both temperatures (Fig. 3, G-tests, $P < 0.05$), but compared with the larger 43-mm fry, the smaller fry were observed more in medium-sized substrate (20–30 mm, G-tests, $P < 0.05$). In general the 32-mm fry showed less pronounced changes in pref-

erences during day and night than larger fry, and the preference values were also more variable. The 32-mm fry in warm water moved significantly more outside, and also above, the substrate patches in daytime compared with the 43-mm fry (G-tests, $P < 0.05$). In cold water they also moved comparatively less to the inlets and outlets at nighttime (Fig. 3).

Discussion

Generally, independent of fry size, brown trout fry showed a strong preference for the coarser substrate compared with the other gravel sizes offered. There seems to be a clearcut reason for this. The coarser the substrate, the better cover represented by the interstitial spaces between the particles, up to an optimum. Evidently the function of the gravel substrate in these experiments was to supply cover and probably also shelter from high water velocities. The smaller substrate size (8–16 mm) could not be entered by brown trout without "digging in," which did not occur to any significant degree. The fewest number of fish was observed on small substrate. The importance of substrate as cover for juvenile salmonids has been emphasized in several field studies (Chapman and Bjornn 1969; Bjornn 1971; Bustard and Narver 1975a, 1975b; Rimmer et al. 1983; Cunjak and Power 1986) and also for Atlantic salmon in experimental studies (Gibson 1978).

Large gravel also provides more low water velocity microniches, which presumably is of adaptive significance (Bachman 1984; Fausch 1984). The fry may also prefer the larger gravel because of the increased visual isolation. Among the territorial brown trout fry, increased visual isolation apparently reduces the agonistic behaviour and thus increases the holding capacity of a stream area (Kalleberg 1958).

Substrate appears to be an important habitat variable for salmonids only when fish can get into the interstices (Bjornn 1971). McCrimmon (1954) reported decreased Atlantic salmon survival with increased sedimentation of the creek bottom. Reduced sandy bedload sediment has been found to result in increased numbers of brown and rainbow trout (Alexander and Hansen 1983). Silted substrate is unsuitable for salmonids, especially at low temperatures (Bustard and Narver 1975b; Hillman et al. 1987).

Brown trout fry of both sizes hid significantly more in the substrate at low temperatures than at high temperatures. Experimental and field studies of trout and salmon have indicated that substrate providing cover and shelter may be more important at low temperatures, and that low temperatures may trigger a daytime winter hiding behaviour and movements to areas with suitable (i.e. coarser) substrate (Hartman 1963; Chapman and Bjornn 1969; Bjornn 1971; Bustard and Narver 1975a; Tschaplinski and Hartman 1983; Cunjak and Power 1986). This was demonstrated in field studies for Atlantic salmon by Rimmer et al. (1983, 1984) and in laboratory studies by Gibson (1978). The threshold temperature seems to lie between 5 and 10°C. Swimming performance of trout fry also decreases at lower temperatures (Webb 1978; Heggenes and Traaen 1988). The reported experimental results suggest that brown trout also have a stronger tendency to seek cover and shelter in the substrate at low temperatures, at least in daytime.

The light conditions also influenced the substrate preferences of the brown trout fry significantly. Both length groups were observed to move more over the substrate and towards the inlets and outlets at nighttime, i.e. in the dark. This was most pronounced for the largest length group. The results support the conclusion that substrate was important as cover in these experiments. The darkness presumably functioned as a cover in itself and substituted for hiding in the substrate interstices.

The reason why I did not observe any consistent differences in behaviour of the fry in daytime at increased water velocities is probably that the tested velocities did not come close to the critical level of sustained water velocities (Ottaway and Forrest 1983; Irvine 1986; Heggenes and Traaen 1988). The decreased number of observations of fish at the inlet at night may reflect a downstream displacement.

The artificial environment and short acclimation period for brown trout in the channels in this study may be a source of error that may limit the application of the results to wild brown trout. With regard to acclimation, Fausch and White (1986) found that young brown and brook trout (*Salvelinus fontinalis*) grew poorly even after up to 2 wk of acclimation in a laboratory stream. However, in their study stream there was no cover affording visual isolation, and that may be the reason for the poor growth. The acclimation period in my experiments was comparable with those used in other experimental studies (DeVore and White 1978; Wilzbach 1985), and the fish were beforehand acclimated to the water supply.

Also, there was no indication in my results that substrate preferences changed during the test period. It is difficult to assess the effect of artificial environment; it may have aggravated the cover-seeking and hiding behaviour of the fish. Differences in food availability may influence substrate choice (Gibson 1978; Rimmer et al. 1984) and cover preferences (Wilzbach 1985), but this could not be investigated here.

The results bear special importance to management plans implemented to improve trout habitat in streams. The fish clearly had the strongest preference for seeking shelter in the coarsest substrate (50–70 mm), which is larger than that considered to be optimal for spawning (10–20 mm). Consequently, it may be important to increase the area with substrate of this preferred size for fry, as well as to provide suitable spawning substrate.

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Validity of an Ecotoxicological Test System: Short-Term and Long-Term Effects of Arsenate on Marine Periphyton Communities in Laboratory Systems

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Periphyton communities were established on glass substratum in the Gullmar Fjord (Sweden) and their sensitivity to arsenate was determined with short-term photosynthesis experiments. The study was done in May 1984 when phosphate levels were low. A 1-h exposure to arsenate gave IC_{20} (concentration required to inhibit photosynthesis by 20%) values of 0.4 μM. Communities established indoors in a flow-through aquaria system were substantially different from the fjord communities in terms of structure and biomass, although photosynthesis showed a similar sensitivity (IC_{20} = 0.6 μM). To explore the validity of this short-term ecotoxicological test system, we used a set of indoor, flow-through aquaria to study long-term effects (3 wk) on communities established under arsenate stress. Arsenate was added continuously at 0.1–10 μM above background levels (7 nM). Species composition as well as carbon, nitrogen, and chlorophyll *a* content of the communities were affected at 0.2–0.8 μM (IC_{20}). This is in good agreement with the sensitivity of the short-term test. We conclude that inhibition of the physiological parameter photosynthesis is relevant information for the understanding of ecological events caused by arsenate stress in the periphyton communities. At least for effects of arsenate, the short-term metabolic test system can be used for valid predictions of gross changes in periphyton community structure and production. Comparison with arsenic levels in polluted coastal areas of Sweden lead to the conclusion that periphyton communities may be affected, particularly when phosphorus levels are low.

Dans le fjord Gullmar (Suède), on a fait croître des communautés de périphyton sur un substrat de verre et leur sensibilité à l'arséniate a été établie par des expériences de photosynthèse de courte durée. L'étude a été effectuée en mai 1984 lorsque les teneurs en phosphate étaient faibles. Une valeur IC_{20} (concentration nécessaire pour inhiber la photosynthèse de 20 %) de 0,4 μM a été enregistrée après une exposition d'une heure à de l'arséniate. Des communautés établies à l'intérieur dans un aquarium à débit continu étaient très différentes des communautés du fjord au niveau de la structure et de la biomasse, bien que la photosynthèse ait présenté une sensibilité semblable (IC_{20} = 0,6 μM). En vue d'étudier la validité de ce système d'épreuve écotoxicologique de courte durée, nous avons utilisé un ensemble d'aquariums intérieurs à débit continu afin d'étudier les effets à long terme (3 sem) sur les communautés qui se sont établies tout en étant exposées à l'arséniate. De l'arséniate a été ajouté continuellement à raison de 0,1–10 μM de plus que les taux naturels (7 nM). La composition des espèces ainsi que la teneur en carbone, en azote et en chlorophylle *a* des communautés ont été modifiées lorsque la concentration était comprise entre 0,2 et 0,8 μM (IC_{20}). Ces données concordent avec la sensibilité de l'épreuve de courte durée. Il ressort que l'inhibition de la photosynthèse, paramètre physiologique, constitue une donnée pertinente permettant de comprendre les phénomènes écologiques provoqués par une exposition à l'arséniate des communautés du périphyton. Au moins pour les effets de l'arséniate, le système d'épreuve métabolique de courte durée peut être utilisé pour formuler des prévisions valables de modifications macroscopiques au niveau de la structure et de la production de la communauté du périphyton. Une comparaison des taux d'arsenic dans les zones côtières polluées de la Suède a permis de conclure que les communautés du périphyton peuvent être touchées, notamment lorsque les taux de phosphore sont faibles.

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Ecotoxicological test systems can be used to identify potential impact of pollutants before damage occurs in the ecosystems. Community- or ecosystem-level testing was advocated by the National Research Council (1981) as the only strategy available to obtain ecologically relevant information, and a variety of sophisticated model ecosystems are used in studies of aquatic pollution (Lundgren 1985). However, to become efficient tools, these community- and ecosystem-level tests must also be designed for a high test capacity. It will not be sufficient to test only a handful of chemicals per year. Short-term testing should therefore be preferred. Also, the critique raised against multitier test strategies (Cairns 1983) emphasizes the need to develop short-term test systems capable of generating ecologically relevant information.

Structural changes of affected communities develop too slowly for short-term experimentation whilst metabolic activities, such as photosynthesis or respiration, usually respond to pollutants within a few hours. Based on the rationale that effects

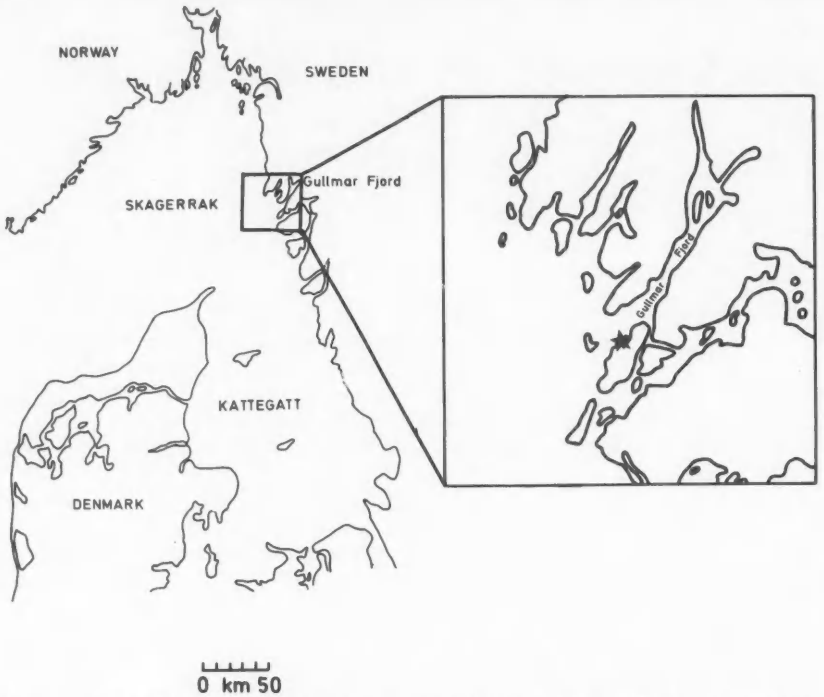

FIG. 1. Location of the Gullmar Fjord on the west coast of Sweden. The water intake and periphyton reference station are located in Smalsund, close to Kristineberg Marine Biological Station (star).

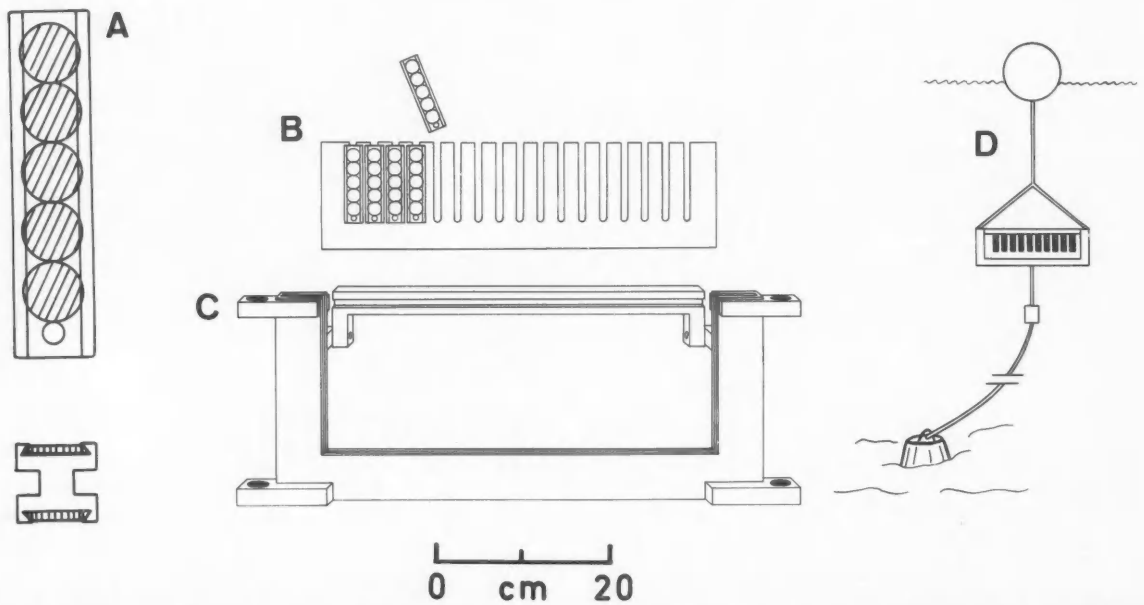

FIG. 2. Periphyton sampling device. The sampling units were circular glass discs (thickness 1 mm, diameter 14.5 mm) mounted on disc holders (A). The holders were inserted into a rack (B), which was supported by a special frame (C). At the reference station in the Gullmar Fjord the rack hung at 2 m of depth (D). Holders, racks, and frames were all made of polyethylene.

on metabolism are indicative of changes in structure and production and lead to long-term effects in the community, we developed a periphyton test system designed to measure short-term effects on photosynthesis (Blanck 1985). Krock (1972) and Orhon (1975) used similar approaches. The rationale behind the periphyton test system is discussed in more detail in Blanck (1983).

The small size of the periphyton samples and the short test duration are convenient for investigating effects of chemicals on complex communities. The test system we outline is not dependent on any specified test organism and can be used in various environments with maintained ecological realism because the periphyton community that actually will receive the pollutant can be sampled and need not be represented by other organisms. The approach concurs with the suggested use of system-level properties, such as processes in biogeochemical cycles, as test parameters in test systems excised as intact units from natural communities (O'Neill and Waide 1981). They argued that the organisms will thus be tested in their natural association with other organisms with whom they share evolutionary history. Also, Warren and Liss (1977) emphasised the close connections developed through coevolution of members within a community, when they suggested a distinction to be made between multispecies and community-level test systems.

Ecotoxicological test systems must be validated before any reliable conclusions can be drawn from the generated data. A crucial point for the validity of the periphyton test system is the anticipated relationship between short-term effects on metabolism and the long-term effects on community structure and function. This relationship has as yet not been experimentally examined and the predictive value of the periphyton test system is currently unknown.

The present study employs arsenate to test whether inhibition of periphyton photosynthesis in short-term experiments is relevant for a prediction of longer-term effects on species composition and net community production.

Materials and Methods

Experimental Site

The reported experiments were done in May 1984 at Kristineberg Marine Biological Station (KMBS) by the Gullmar Fjord on the west coast of Sweden (Fig. 1). Three distinct water masses are usually present in the fjord (Lindahl 1987): (1) a nutrient-rich, high-saline deep water below the sill depth, (2) a coastal surface water with a salinity of 20–25‰ which in May is low in nutrients, and (3) an intermediate depth (15–40 m), with intermediate nutrient and salinity levels, a water of Skagerrak origin. The hydrography of the Gullmar Fjord was summarized by Svansson (1984).

Periphyton Sampling

Periphyton communities were sampled by submerging artificial substrata either in the fjord or in a flow-through indoor

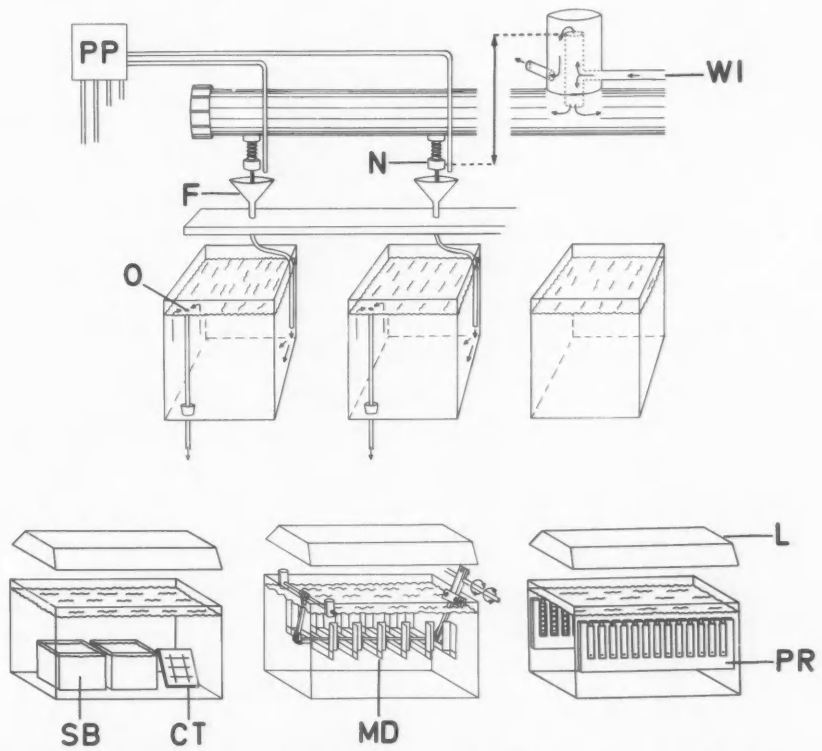

FIG. 3. Aquaria system used for colonization of periphyton under arsenate stress. The vertical arrows indicate the variable height of the water column generating the hydrostatic pressure. WI, water intake; N, nozzle; PP, peristaltic pump; F, funnel; O, overflow; L, lamp; SB, sediment boxes; CT, ceramic tiles; PR, periphyton racks; MD, mixing device. See Materials and Methods section for explanations.

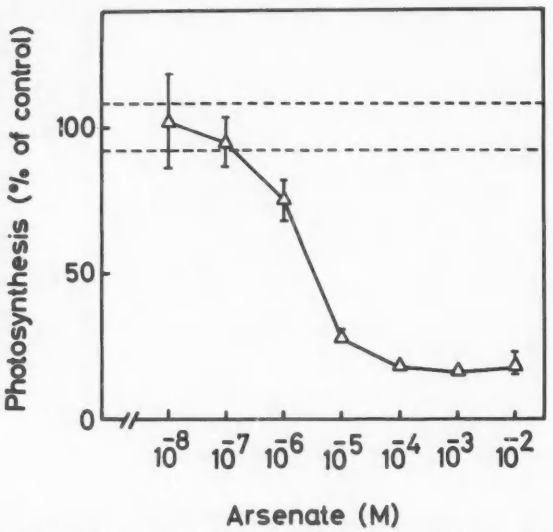

FIG. 4. Inhibition of photosynthetic activity by arsenate in a marine periphyton community. The indoor control community was exposed to background concentrations of arsenate (7 nM) during the colonization period. Prior to measurement of photosynthesis the community samples were incubated with arsenate for 1 h. Phosphate concentration in the incubation medium was 0.05 μM. Average chlorophyll *a* content of the discs was 9.0 μg. Vertical bars show standard deviations. The broken horizontal lines show the 95% CI for the photosynthetic activity of untreated periphyton samples (n = 5).

TABLE 1. Quotient of similarity between the periphyton communities established under various degrees of arsenate stress. All communities were compared with the indoor community established at background levels of arsenate. Three periphyton discs were analyzed from each type of community and the data pooled.

Type of community	Quotient of similarity
Reference community	0.32
Control community	1.0
0.1 μM arsenate	0.67
0.3 μM arsenate	0.57
1.0 μM arsenate	0.53
3.2 μM arsenate	0.42
10 μM arsenate	0.29

aquaria system where arsenate concentrations were manipulated. The sampling units (Fig. 2) were circular glass discs with an area of 1.5 cm^2. The discs were mounted in disc holders inserted into racks, each of which contained 170 discs when both sides of the holders were occupied. The racks were supported by a robust frame when sampling in the fjord and by simple holders when used in the indoor aquaria. The periphyton sampling device was hung from a buoy at a reference station in Smalsund just outside KMBS at a depth of 2 m (Fig. 2).

Arsenate Exposure and Aquaria System

Fjord water with its indigenous microbiota was pumped into the laboratory from a depth of 6 m. The system of Granmo and Kollberg (1972) was used to establish a continuous flow of water (200 $mL \cdot min^{-1}$) through a set of 24 glass aquaria (Fig. 3). The flow rate yielded a mean residence time of about 100 min in each aquarium. A coarse filter at the water intake was used to retain particles that could interfere with water flow through the nozzles. The flow rate was controlled by the diameter of the nozzles and the hydrostatic pressure which was adjusted by the position of the nozzle. The water level in each aquarium was held constant by an overflow. Arsenate stock solutions, delivered by means of a peristaltic pump (Ismatech MP 25), were mixed with seawater in funnels to give nominal arsenate concentrations in the aquaria of 0, 0.1, 0.32, 1.0, 3.2, and 10 μM above background; the background concentration of arsenic was 7 nM. Flow rates of water and stock solutions were checked regularly and adjusted to maintain the desired values. Four replicate aquaria were used for each exposure level. The accuracy of the dosing was checked by analysis of total arsenic using automated hydride generation and flameless atomic absorption spectrometry (cf. Borg et al. 1985). Nominal and analyzed concentrations of arsenic in the aquaria were similar, within ± 10%.

Each aquarium was illuminated from above by two fluorescent tubes (Osram L 40W/19 Daylight 5000 de luxe) to give a photon flux density (400–700 nm) at the water surface of 125 $\mu E \cdot m^{-2} \cdot s^{-1}$. The light period was changed once weekly to simulate actual daylength. Water temperature in the aquaria was about 0.5°C higher than the water temperature at the reference station.

Two racks containing 170 glass discs were placed along the sides of each aquarium (Fig. 3). To increase nutrient uptake by periphyton in the aquaria, some turbulence was generated by a reciprocal-motion mixing device. Unglazed ceramic tiles and a glass box filled with sediment were placed between the racks for colonization by hard- and soft-bottom fauna, respectively (Granmo et al., unpubl. data).

Water Chemistry

Temperature and salinity of the incoming water from various depths are measured daily at KMBS. These data were used to detect water exchanges in the fjord influencing water quality in our systems. Nonparticulate, molybdate-reactive phosphate (Koroleff 1976) was measured occasionally in the incoming water and in all reaction media used in the photosynthesis experiments.

Photosynthesis Experiments

Photosynthetic activity of the periphyton was measured as incorporation of radiolabelled carbon dioxide. Periphyton samples were collected either from the fjord or from the aquaria immediately before the start of an experiment. A set of discs similar in gross appearance was selected to ascertain similar biomass and photosynthetic activity among the replicates. The periphyton samples were preincubated for 60 min in glass scintillation vials, each containing 2 mL of test solutions made from filtered seawater (Whatman GF/F). A geometric concentration series (factor 10) of arsenate from 10 nM to 10 mM was used in each test with three replicates of each arsenate concentration. The control responses were evaluated using five replicates. The samples were gently stirred by shaking during the preincubation period. The incubator was thermostated to the temperature at the sampling site (9–10°C) and equipped with six 150-W Atralux lamps (Osram). The light was passed through 20 cm of water and grey Perspex filters to give an irradiance of 125 $\mu E \cdot m^{-2} \cdot s^{-1}$. At the end of the preincubation period, 50-μL aliquots of $NaH^{14}CO_3$ (2 μCi (74 kBq), 1.9 mM) were added to each of the 26 vials at 10-s intervals. After 15 min for incorporation of the ^{14}C, photosynthesis was stopped by removing

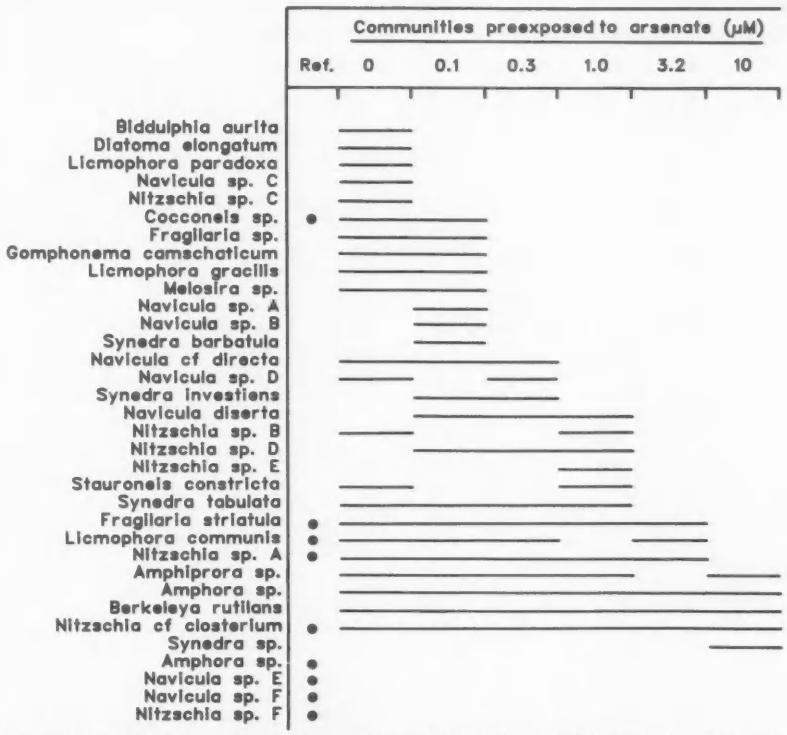

FIG. 5. Diatom species present in marine periphyton communities established on glass discs under background and elevated arsenate concentrations. The species are arranged in order of increasing tolerance to arsenate. The references community (Ref.) was established in the fjord; the other communities were from indoor aquaria. Nominal arsenate concentrations above background are given. Note the differences between the two communities established at background levels. Capital letters after generic names designate separate forms that were not identified to species. The colonization period was 3 wk.

the seawater with a suction pump and adding 1 mL of concentrated acetic acid. The remaining carbon dioxide was thus driven off and the residue dried at 60°C. Periphyton was dissolved by adding 0.3 mL of distilled water and 1 mL of tissue solubilizer (Soluene 350, Packard Instrument Company Inc.). Ten millilitres of scintillation cocktail (Omnifluor, New England Nuclear, in toluene) was then added and the samples were thoroughly mixed. The amount of ^{14}C incorporated was determined with a Packard Tricarb liquid scintillation spectrometer (model 3255) with external standard ratio procedures to correct for quenching. Formalin-killed periphyton incorporated ^{14}C activity corresponding to about 100 dpm, a value which was subtracted from all readings.

Determination of Biomass and Species Composition

Periphyton was sampled for biomass and species composition after a colonization period of 3 wk. Several periphyton discs were pooled before the duplicate biomass determinations. Chlorophyll *a*, used as an index of algal biomass, was extracted in dimethyl sulfoxide at 65°C for 30 min (Hiscox and Israelstam 1979). The chlorophyll *a* concentrations were calculated from its absorption assayed in 1:1 dimethyl sulfoxide and 90% acetone (Shoaf and Lium 1976) using the equations of Jeffrey and Humphrey (1975). Samples for total carbon and total nitrogen were prepared from periphyton scraped from the surface of the discs and analyzed with a Carlo-Erba model 1106 elemental analyzer (Blanck 1985). Taxonomic analyses of the diatom-dominated periphyton communities were made using fresh and ethanol-fixed samples. In the latter case, the samples were put into 70% ethanol and kept at 4°C until being oxidized with concentrated nitric acid. The abundance of diatoms was determined semi-quantitatively using a three-graded scale, where 1 = rare species and 3 = dominating species. A quotient of similarity between communities was calculated according to Sørenson (1948).

IC_{20} Determinations

Since no generalized view is available on the shape of dose–response curves for periphyton communities, it is not justified to adopt common models for inhibitory concentration (IC) value estimation. The IC values were therefore determined by geometric interpolation only.

Results

The inhibitory effect of arsenate on periphyton photosynthesis occurs in less than 30 min (Blanck et al., unpubl. obs.) and a standard preincubation time of 1 h was therefore chosen to ensure full inhibition. Photosynthesis of periphyton communities was reduced by arsenate at less than 1 μM after a 1-

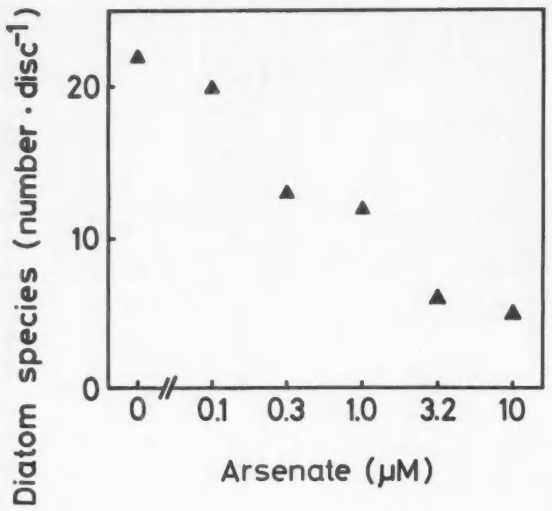

FIG. 6. Number of diatom species present in indoor periphyton communities established under various degrees of arsenate stress. The colonization period was 3 wk.

h exposure (Fig. 4), but a 15–20% fraction of the photosynthetic activity could not be inhibited even at 10 mM arsenate. Although the level of this plateau varied somewhat from experiment to experiment, the presence of the plateau in the concentration–effect curve is characteristic of all our studies of arsenate and marine periphyton. All communities established at background levels of arsenate and at low nutrient levels were similar in terms of their sensitivity to added arsenate, no matter whether the community was taken from the indoor aquaria or from the reference station in the fjord. In May 1984, IC_{20} (the concentration of a toxicant needed to inhibit photosynthesis by 20%) was 0.4 μM for the former and 0.6 μM for the latter community, even though the two communities differed substantially in terms of species composition (cf. Table 1; Fig. 5) and algal biomass. For instance the chlorophyll content per disc was 45 times greater in the aquaria than at the reference station but the IC_{20} differed only by a factor of 1.5. Thus, the short-term metabolic test system indicated that the communities would be affected by arsenate concentrations of about 0.5 μM. After 3 wk of colonization and growth, the indoor communities were examined for long-term effects of arsenate on species composition, algal biomass, and primary productivity. Species composition of periphyton communities established under arsenate stress differed from the control communities (Table 1; Fig. 5). A few rare species were excluded by the lowest tested arsenate concentration (0.1 μM), while others tolerated, or were favoured by, 10 μM arsenate under the prevailing conditions. The span in arsenate tolerance among the periphyton species thus exceeded 2 orders of magnitude. The number of diatom species decreased from 22 in the control community to 6 at the highest arsenate concentration (Fig. 6). Arsenate was a significant structuring factor in the periphyton communities at concentrations higher than or equal to 0.3 μM.

Algal biomass (chlorophyll *a*) was reduced by arsenate at 0.3 μM, while total carbon and total nitrogen on the discs were reduced at somewhat higher concentrations (Fig. 7). As arsenate stress increased, carbon to nitrogen ratios declined from 10.5 to 7.3 (Fig. 8). Significant effects on biomass parameters again occurred at 0.3 μM arsenate and higher in the 3-wk-old communities. Although biomass of older communities was not measured, it was observed that biomass differences between control and arsenate-stressed periphyton visually appeared to decrease with time, suggesting that the effect of arsenate on biomass was transient.

Primary productivity of the periphyton communities, measured as the amount of ^{14}C incorporated per disc after the 3 wk of colonization, showed a dependence on arsenate exposure similar to that of chlorophyll *a*. When expressed on a chlorophyll *a* basis rather than on an areal basis, the primary productivity was similar in all indoor communities except those established under the most severe arsenate stress.

To facilitate comparison, IC_{20} values were estimated for all short-term and long-term effect variables (Table 2). The short-term IC_{20} values for inhibition of photosynthesis by arsenate ranged from 0.4 to 0.6 μM, while the long-term IC_{20}-values for species composition and net community production ranged from 0.2 to 0.8 μM. We conclude that the predicted and observed levels of arsenate required to cause long-term effects are in good agreement.

Discussion

Validity of the Periphyton Test System

In this paper we show that short-term toxicity tests with periphyton communities yield meaningful information for the assessment of long-term effects by arsenate on community structure and production (Table 2). Using the terminology of Blanck (1984) the predictive value can be calculated as the ratio between the sensitivity of the predictant and the predictor. In this study the predictor is the sensitivity of the short-term test (i.e. an IC_{20} = 0.4–0.6 μM). The predictant is the sensitivity of the long-term tests (IC_{20} = 0.2–0.8 μM). A perfect match between predictor and predictant generates a value of unity. The observed predictive value for arsenate was 0.3–2.0. For comparison, the predictive value for extrapolation of EC values from a green alga (*Scenedesmus quadricauda*) to a blue-green (*Microcystis aeruginosa*) ranged from 0.013 to 316 for 100 studied chemicals (Blanck 1984). Short-term photosynthetic activity of periphyton communities thus has a high predictive value in assessing long-term effects of arsenate on periphyton. At present we cannot make an overall estimate of the predictive value of the periphyton test because the validation effort has been made using only one compound. It appears, however, that the periphyton test system can be used for certain applications such as determining the seasonal or geographical variation in sensitivity to arsenate, information which should be required in advanced hazard assessment procedures.

A thorough validation of ecotoxicological test systems should demonstrate that a test system yields (or is likely to yield) correct predictions of the sensitivity of one or more ecosystem components. Blanck (1984) suggested that a thorough validation must also involve a large number of representative chemicals to demonstrate that valid predictions can be generated for any chemical assessed. In this respect, no community level test system has, to our knowledge, yet been validated.

In our investigation we compared two aspects of diatom-dominated periphyton communities: the short-term (1 h) responses of photosynthesis and the long-term (3 wk) response

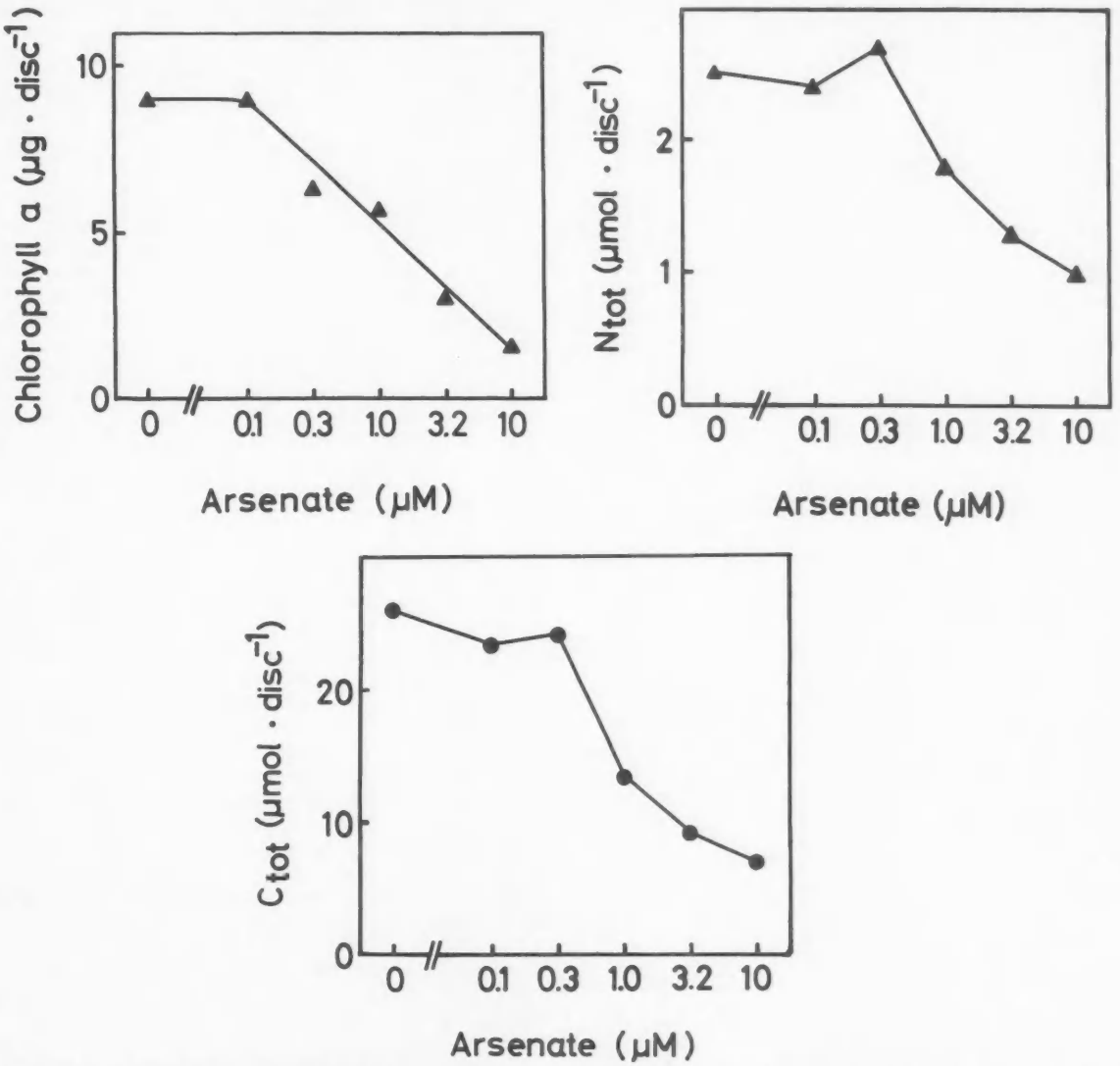

FIG. 7. Biomass of periphyton communities established in indoor aquaria under various degrees of arsenate stress. The colonization period was 3 wk. The points represent means of duplicate samples, each containing several discs.

of community structure and biomass. This approach to validation of the test system allowed us to examine the relationship between the short-term and long-term responses; the latter is intuitively considered the ecologically more relevant, and the former has advantages in terms of simplicity and a higher test potential. The good agreement between the two data sets suggests that ecological relevance, technical simplicity, and a high test potential indeed can be achieved in the same test system.

The periphyton communities investigated in this study were established on glass substrata in a fairly short (3 wk) period of time. This approach may bias results because the sampling method is likely to select mainly for opportunistic species. Although investigators have studied the influence of colonization time and various natural and artificial substrata on community structure, none has considered the possible impact of these parameters on the sensitivity of periphyton to xenobiotics. These questions must be considered when inferences are made about the ecotoxicity of arsenate using the periphyton test system.

Toxicity of Arsenate

Large interspecies differences (2–3 orders of magnitude) in algal sensitivity to arsenate have been observed in algal growth tests (Planas and Healey 1978; Blanck et al. 1984). This study shows that interspecies differences in sensitivity are expressed also under more ecologically realistic conditions. The ratio between the arsenate concentration eliminating the most sensitive algae and the highest concentration tested, which was

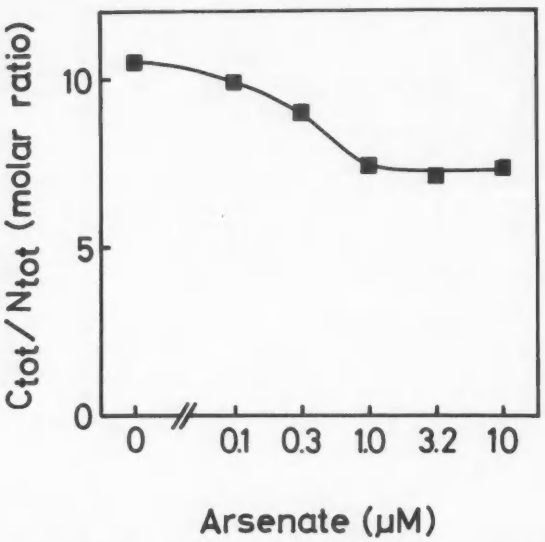

FIG. 8. Carbon to nitrogen ratios in periphyton communities established in indoor aquaria under various degrees of arsenate stress. The colonization period was 3 wk.

TABLE 2. Sensitivity of marine periphyton communities to arsenate, based on various short- and long-term test parameters. The communities were established in indoor aquaria or at a reference station in the fjord. All measurements were made using communities 3 wk of age. The sensitivities of each parameter to arsenate are expressed as IC_{20}-values (i.e. the concentration of arsenate required to reduce an activity or a factor by 20% relative to the control).

Test parameter	IC_{20} (μM arsenate)
Short-term effects	
Reference community	0.4
Control community	0.6
Long-term effects	
Species composition	0.2[a]
Chlorophyl *a* accumulation	0.3
Total carbon accumulation	0.5
Total nitrogen accumulation	0.8
Photosynthesis per unit area	0.3

[a]The number of species was treated as a continuous variable when calculating the IC_{20}.

tolerated by several species in the long-term test, exceeds 2 orders of magnitude (Fig. 5). The variation in sensitivity between various algae in the community is also evident from the concentration–effect curve for community photosynthesis (Fig. 4). The sensitivity of photosynthetic activity to arsenate spans 5–6 orders of magnitude, and there is a 15–20% fraction of photosynthetic activity that is insensitive to 10 mM arsenate, which is almost at saturating levels in marine waters. This broad range in sensitivity can, however, be due to reasons other than interspecies differences. Also, the metabolic state (and particularly the nutrient status) of the algae can modify their sensitivity to arsenate.

The periphyton communities were very similar in their sensitivity to arsenate, provided they had been established in a similar water quality. However, episodes of high nutrient levels were associated with increased arsenate tolerance due to arsenate-phosphate interactions (S-Å. Wängberg and H. Blanck, unpubl. data). The modification of arsenate toxicity by phosphorus is well documented for pure cultures of algae (Blum 1966; Planas and Healey 1978; Sanders 1979) and is due to the competition between phosphate and arsenate for various biochemical sites.

In May 1984, phosphate concentration in the surface water was at its minimum (<0.1 μM) and the effects of arsenate on periphyton occurred at 0.2–0.8 μM (Table 2). This is 25–100 times higher than reported background levels (7–9 nM) of total arsenic in Swedish coastal waters (Andreae and Froelich 1984; this study). The Bothnian Bay of the Baltic Sea is polluted by metal outfall from a smelter. Surface water arsenic concentrations of about 0.6 μM are not rare at distances less than 3 km from this source. Assuming that the arsenate fraction is 80–93% of total arsenic, which usually is the case in oxygenated surface waters (National Research Council of Canada 1978), the arsenate concentration would be about 0.5 μM. Based on our study, such an arsenate exposure could affect primary production and species composition of the periphyton during periods of maximum sensitivity. Environments where algae are limited by phosphorus, such as the Bothnian Bay (Alasaarela et al. 1986), would be even more vulnerable to arsenate pollution. We conclude that arsenate is likely to affect algal communities in the arsenic-contaminated coastal waters of Sweden, particularly during periods when phosphorus concentrations are low.

The primary targets of arsenate in plants are often considered to be photophosphorylation (Avron and Jagendorf 1959), oxidative phosphorylation (Bertagnolli and Hanson 1973; Wickes and Wiskich 1975), or other interference with phosphorus metabolism (Planas and Healey 1978) such as the uptake of phosphate over the plasmalemma (Blum 1966).

We have found that algal photosynthesis responds more rapidly and more markedly than algal respiration to arsenate stress. A primary effect on photosynthesis is consistent with the idea that arsenate interferes with photophosphorylation, which has been shown for chloroplasts of higher plants (Avron and Jagendorf 1959) and chromatophores of photosynthetic bacteria (Melandri et al. 1970; Slooten and Nuyten 1983). The similarity between photosynthetic activity and the long-term test variables in terms of the sensitivity to arsenate (Table 2) further suggests that photosynthesis is a principle metabolic target system of arsenate in algae.

Our results with marine periphyton thus are consistent with the interpretation that arsenate per se is responsible for the toxicity and that the primary target of arsenate in algae is in photophosphorylation. However, because arsenic metabolism is complicated and involves a variety of biologically active intermediates (Andreae 1983; Zingaro and Bottino 1983), other possibilities cannot be ruled out. It has been demonstrated, for example, that the ADP-arsenate formed in bacterial photophosphorylation is stable enough for sugar arsenate to be formed (Slooten and Nuyten 1983) and that sugar arsenates can substitute for the corresponding sugar phosphates in various enzymatic reactions (Lagunas 1980). The significance of these reactions is not well understood. Algae are also able to reduce As(V) (arsenate) to As (III) (arsenite) (Blasco 1975; Matsuto et al. 1984), which can inhibit various enzymes by its binding to thiol groups of the proteins (Latzko and Gibbs 1969; Scarborough 1975). Photosynthesis, for example, is affected by arsenite through inhibition of ribulose-5-phosphate kinase (Latzko and Gibbs 1969) and of the light activation of other key enzymes

in the Calvin cycle (Marques and Anderson 1986). Other arsenic compounds (such as various methylated species), some of which can be synthesized by algae (Andreae and Klumpp 1979; Wrench and Addison 1981; Baker et al. 1983), are also biologically active (Knowles and Benson 1983). All these arsenic compounds may become toxicologically more important to algae under conditions of high nutrient levels when the arsenate toxicity is reduced.

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Induced Community Tolerance in Marine Periphyton established under Arsenate Stress

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Blanck, H., and S-Å. Wängberg. 1988. Induced community tolerance in marine periphyton communities established under arsenate stress. Can. J. Fish. Aquat. Sci. 45: 1816–1819.

Pollution-induced community tolerance (PICT) may be used to assess impact of pollutants in the environment and to identify the agents causing the impact. We have examined this possibility using marine periphyton communities. These were established under arsenate stress in indoor aquaria and their community tolerance to arsenate estimated with a short-term photosynthesis test. Arsenate concentrations above 0.1–0.3 μM induced an increased tolerance to arsenate; at severe arsenate stress the increase in tolerance was more than 17 000-fold. Our interpretation is that arsenate exerted a selection pressure on the community, leading to the replacement of sensitive species by tolerant ones which caused the overall arsenate tolerance of the community to increase. Arsenate concentrations that induced the tolerance also affected species composition and biomass accrual, suggesting that community tolerance can be used to properly indicate a disturbed community. Hence the basic requirements are met for the use of PICT as an ecotoxicological tool.

La tolérance de la communauté induite par la pollution peut être utilisée afin d'évaluer les répercussions des polluants dans le milieu et d'en déterminer les agents responsables. Cette possibilité a été étudiée à l'aide des communautés marines composant le périphyton. Ces communautés se sont établies dans des aquariums intérieurs où elles étaient exposées à de l'arséniate et leur tolérance à ce produit a été déterminée au moyen d'une épreuve de photosynthèse de courte durée. Des concentrations d'arséniate supérieures à 0,1–0,3 μM ont induit une tolérance accrue à l'arséniate; lorsqu'elles étaient exposées à des concentrations importantes, la tolérance des communautés à l'arséniate était augmentée de plus de 17 000 fois. À la lumière de ces résultats, nous pensons que l'arséniate a exercé une pression de sélection sur la communauté, ce qui a entraîné le remplacement des espèces sensibles par des espèces tolérantes qui ont fait augmenter la tolérance générale de la communauté à ce produit. Des concentrations d'arséniate qui ont induit la tolérance ont également modifié la composition des espèces et l'accroissement de la biomasse, ce qui semble indiquer que la tolérance de la communauté peut constituer un bon indicateur de perturbation de la communauté. La tolérance de la communauté induite par la pollution peut donc être utilisée comme outil écotoxicologique puisqu'elle répond aux exigences de base.

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In response to the difficulties in determining whether or not trace contaminants present in an environment have adversely affected biota, Luoma (1977) suggested that the development of resistance to a toxicant by a population is direct evidence that the toxicant exerts a selection pressure on the species at that location. Additionally, Luoma (1977) argued that resistance to one toxicant, but not to others to which the population is exposed, suggests that the former contaminant is the cause of the biological damage.

If these points are true, analyses of induced tolerance at the population or community levels could be used to assess the impact of pollutants in the environment and to identify the agents causing the impact. We have applied this idea to periphyton algae at the community level. However, the concept is based on several assumptions that need experimental verification. For example, the tolerance increase must be correlated with other indicators of biological damage, and the specificity of the selection pressure must be high enough to allow a discrimination between different toxicants.

The most fundamental prerequisite, that tolerance *is* induced in algae, is beyond doubt. The presence of metal-tolerant algal populations (or strains) in polluted environments was shown by Stokes et al. (1973) and Jensen et al. (1974), and the development of tolerance was later demonstrated for a variety of algal species (e.g. Harding and Whitton 1976; Gavis et al. 1981; Foster 1982; Reed and Moffat 1983; Murphy et al. 1982; Cosper et al. 1984). The presence of metal-tolerant strains appears to be widespread in metal-polluted environments (Stokes 1983). In algal cultures, tolerance can develop after long-term exposure to constant or succesively higher concentrations of toxicants (e.g. Kellner 1955; Stockner and Antia 1976; Whitton and Shehata 1982). Whether the tolerance is acquired by phenotypic (physiological adaptation) or genotypic changes (selection) in the algal population is usually not sorted out conclusively. In principle, both strategies are possible.

In a community, interspecific selection can also occur. Pollutants affecting communities cause a decrease in diversity by exclusion of sensitive species, or by replacement with tolerant or opportunistic ones (Pearson and Rosenberg 1978; Gray 1979; Sheehan 1984). In the CEPEX experiments, copper was added to a planktonic community in large enclosures and the replacement of sensitive species by less sensitive ones led to the development of a copper-tolerant phytoplankton assemblage (Thomas and Seibert 1977; Harrison et al. 1977). It is reason-

able to expect a similar response to toxicants by other algal communities.

The aim of the present paper was to examine the basis for an application, at the community level, of induced tolerance as an ecotoxicological tool. We wanted to determine (1) whether toxicant stress of a periphyton community leads to an increase of that community's tolerance, (2) whether there is a relationship between the induced tolerance in algal communities and gross effects of the pollutant on community structure and function, and (3) whether the level of community tolerance can be meaningfully measured by the short-term periphyton test system proposed by Blanck (1985) and Blanck and Wängberg (1988).

Materials and Methods

Surface water from the Gullmar Fjord (on the west coast of Sweden) with its indigenous microbiota was pumped into the laboratory at Kristineberg Marine Biological Station (in May 1984) and allowed to continuously flow through a set of aquaria containing samplers for periphyton to colonize. Marine periphyton communities were established under arsenate stress on artificial substrates (circular glass discs with an area of 1.5 cm^2) in the aquaria, as described by Blanck and Wängberg (1988). The nominal concentrations of arsenate in the aquaria were 0.1–10 μM. The background levels were around 7 nM.

The so established periphyton communities, developed under various degrees of arsenate stress, were compared in terms of their community tolerance to arsenate. These experiments were done after 2–3 wk of periphyton colonization and growth. The arsenate tolerance was determined by a short-term photosynthesis test (Blanck and Wängberg 1988).

The glass discs, upon which the periphyton grew, were preincubated (1 h) in glass scintillation vials, each containing 2 mL of GF/F-filtered seawater with the desired arsenate concentration (10 nM to 10 mM above background). Each test employed seven arsenate concentrations in triplicate. To evaluate the response of untreated control samples, five replicates were used. Photosynthetic activity of the communities was measured as the incorporation of ^{14}C into acid-stable components during 15 min, immediately after the 1-h preincubation period. The radioactivity values, obtained by liquid scintillation counting, were corrected for ^{14}C activity in formalin-killed periphyton samples included in every experiment.

A pair-wise comparison of dose–response curves was done with a two-way ANOVA procedure (Sokal and Rohlf 1981). A significant interaction component indicates that the two curves are different. To obtain equal variance for all treatments, the logarithms of the photosynthetic activities were used in the ANOVA analyses.

IC_{20}-values (i.e. the concentration of arsenate required to reduce the photosynthetic activity by 20%) were estimated by geometric interpolation.

Results

Each of the periphyton communities, established under various degrees of arsenate stress, were assayed by the short-term photosynthesis test to determine their tolerances to arsenate. The slopes of the concentration–effect curves (Fig. 1) were gentle (covering 3–5 orders of magnitude) with a distinct plateau at the highest concentrations. Even communities not preexposed to arsenate had a small fraction (15–20%) of photosynthetic activity that could tolerate as much as 10 mM arsenate. A long-term preexposure to arsenate increased this fraction, and in communities that developed at preexposure levels >1 μM arsenate, essentially no effects of arsenate on photosynthesis could be observed. All communities established under arsenate stress differed significantly from the control communities in terms of arsenate tolerance (Table 1). The most tolerant communities had IC_{20} values >10 mM arsenate. The control and reference communities that developed at background levels of

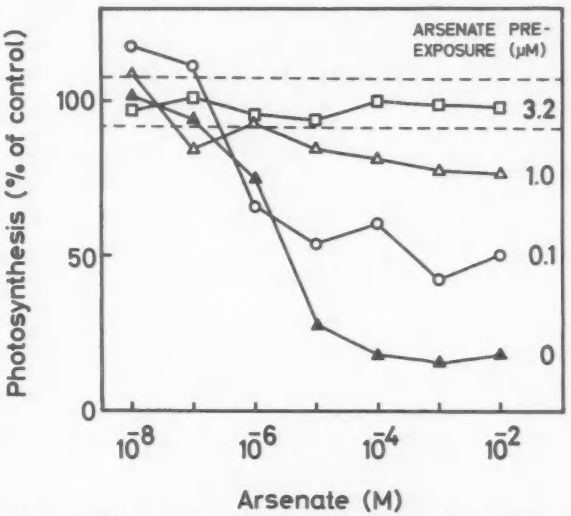

FIG. 1. Inhibition of photosynthesis by arsenate in various periphyton communities established under different degrees of arsenate stress. Prior to measurement of photosynthesis, the samples were incubated for 1 h at the arsenate concentrations given on the *x*-axis. The different sets of periphyton samples differed in biomass and activity, and therefore, relative photosynthetic activities are given. Within each set, 100% activity represents the mean photosynthetic activity of those samples that were incubated at background arsenic levels during the short-term test. Each point is the mean of three (arsenate exposed) or five (control) replicates. The broken horizontal lines show the 95% CI for the photosynthetic activities of periphyton exposed to background levels of arsenic during the colonization and photosynthesis experiments. The phosphate concentration in the incubation medium was 0.05 μM.

TABLE 1. Pairwise comparisons, using two-way ANOVA, of the response to arsenate of periphyton communities established under various degrees of arsenate stress. *p*-values for the interaction components are given; n.s. = not significant. Significant interaction indicates that the arsenate pretreatments made the response of the two communities different in the short-term test. The different communities are designated by the nominal arsenate concentrations at which they were established.

	Arsenate (μM)					
	Control	0.1	0.3	1.0	3.2	10
Control						
0.1 μM	<0.001					
0.3 μM	<0.001	n.s.				
1.0 μM	<0.001	<0.005	n.s.			
3.2 μM	<0.001	<0.001	<0.01	n.s.		
10 μM	<0.001	<0.005	<0.025	n.s.	n.s.	
Reference	<0.001	n.s.	<0.01	<0.025	<0.005	<0.05

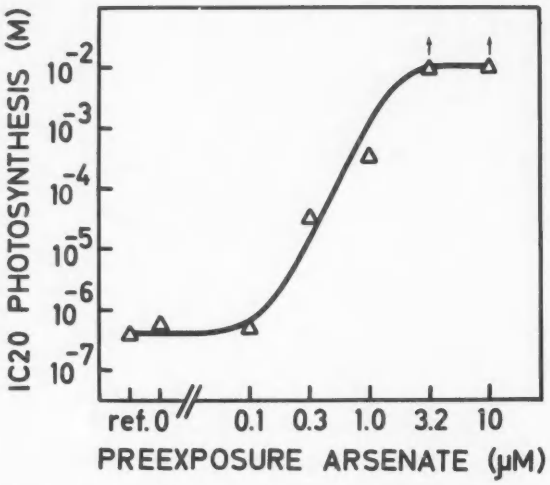

FIG. 2. Relationship between the arsenate tolerance and arsenate preexposure in periphyton communities established under arsenate stress. The tolerance levels are expressed as IC_{20}-values (i.e. the arsenate concentration required to inhibit the photosynthetic activity by 20%) in the short-term test. The two communities established at background levels are designated ref. (reference community from the fjord) and 0 (control community indoors), respectively. Arrows indicate that the concentrations tested were not sufficient to inhibit photosynthesis by 20%. Note the logarithmic scales.

TABLE 2. IC_{20} values for species composition and biomass parameters in marine periphyton established under various degrees of arsenate stress. All measurements were made on communities 3 wk of age (data from Blanck and Wängberg 1988).

Test parameter	IC_{20} (μM arsenate)
Species composition	0.2[a]
Chlorophyll *a* accumulation	0.3
Total carbon accumulation	0.5
Total nitrogen accumulation	0.8

[a]The number of species was treated as a continuous variable when calculating the IC_{20}.

arsenate had IC_{20}-values for inhibition of photosynthesis of 0.4–0.6 μM. In the extreme cases, arsenate tolerance of the communities thus increased by a factor of >17 000.

The relationship between preexposure level and degree of arsenate tolerance appeared sigmoidal (Fig. 2). The levelling off of the curve at the highest preexposure levels is apparent, however, and occurred because IC_{20} values above 10 mM were not estimated. Although the curve shapes of the control differ significantly from the reference and 0.1 μM communities (Fig. 1; Table 1), the IC_{20}-values were similar (0.6, 0.4, and 0.5 μM, respectively). Only at preexposure levels higher than 0.1 μM was the community tolerance in terms of IC_{20}-values affected.

The arsenate-stressed periphyton communities contained fewer species and had lower algal biomass than those exposed to background levels of arsenate (Table 2). Arsenate concentrations of 0.2–0.8 μM reduced the number of species and the carbon, nitrogen, and chlorophyll *a* content of the communities by 20%. A detailed account of these data is given in Blanck and Wängberg (1988).

Discussion

Communities established under arsenate stress were drastically more tolerant to arsenate than those communities established at background levels of arsenate. The large species-dependent variation in arsenate tolerance (Blanck et al. 1984) and the presence of arsenate-tolerant photosynthetic activity (Blanck and Wängberg 1988) suggested that arsenate-tolerant components could be expected in the periphyton, and obviously the applied arsenate stress enabled them to dominate the communities.

The tolerance increase in a community may be due to several different changes taking place simultaneously in response to the stress. Our results do not discriminate between these. It seems likely, however, that the interspecific selection is more important than the selection within populations or the alteration of individual phenotypes, since the tolerance increase coincided with changes in species composition and a lowering of the number of species. The first tolerance increase was seen at arsenate preexposure levels between 0.1 and 0.3 μM (Fig. 2), and in this concentration interval, we also observed the first significant changes in species composition (Blanck and Wängberg 1988). A reasonable interpretation is that arsenate exerted a selection pressure which restructured the community and thereby caused the increase in community tolerance.

There was good agreement between the arsenate level that induced tolerance and that which caused other effects on the community. The range of IC_{20}-values for the long-term test variables was 0.2–0.8 μM (Table 2), suggesting that the induced community tolerance (which appeared at 0.1–0.3 μM) correctly indicated that the community had been affected. These results are the first empirical indication that community tolerance can be used as direct evidence that a community has been affected and restructured by the toxicant. However, early observations from the CEPEX studies (Harrison et al. 1977; Thomas and Seibert 1977) can be interpreted in a similar way.

Luoma (1977) suggested that induced tolerance in a population is direct evidence that the *population* was affected by the toxicant. However, any extrapolation to the community as a whole will have to rely upon the assumption that other community members as well are likely to have been affected. The community tolerance approach proposed here requires no such assumption, since any change in the community structure due to the selection pressure exerted by the toxicant should be expressed as an increased tolerance level. This property is one of the major advantages gained by using community tolerance instead of the tolerance of individual populations. Another advantage with the former is that it makes use of the interspecific variation in sensitivity and not only the variation within a species. The potential tolerance increase is therefore likely to be greater.

The tolerance and preexposure levels were related but the induced tolerance levels were always much higher (100- to 1000-fold) than the corresponding preexposure levels. Hence, there was a certain overcapacity in the community tolerance. If an arsenate-sensitive species is eliminated and is replaced by a species only slightly less sensitive, this outcome would not be expected. Instead, it appears that arsenate-sensitive species were replaced primarily by community members with the highest tolerances. This type of response is advantageous for the use of community tolerance as an ecotoxicological tool. Community tolerance should be sensitive because it scans the community for its most sensitive components, and it would be easily

detected because the most sensitive components seem to be replaced by the most tolerant ones. Community dynamics thus seem to amplify the response to a toxicant.

The degree of tolerance was estimated using a short-term metabolic test. That the effect of arsenate on photosynthesis should properly reflect the arsenate tolerance of the periphyton in more general terms is not self-evident. In the present case, however, the approach is justified by several observations indicating similar sensitivity of a variety of test variables (Fig. 2 and table 1 in Blanck and Wängberg 1988).

Obviously, photosynthesis can be used to estimate the arsenate tolerances of various periphyton communities. The observed consistency strengthens the argument that the effect of arsenate on algae is primarily on photosynthesis (Blanck and Wängberg 1988). Indeed, it may be a prerequisite for this approach to be successful that the tolerance levels are determined by a test representing the physiological process that is the primary target of the toxicant. At present, we do not know if a test parameter responding only secondarily, i.e. due to the breakdown of another metabolic system, can be used to correctly measure the community tolerance. If this is not the case, a battery of short-term metabolic tests would be required.

We have demonstrated that community tolerance of periphyton does increase in response to arsenate stress, and that the degree of increase is easily detected. The tolerance increase coincides with changes in species composition and net production, and hence can be used as an indicator of a disturbed community. The community tolerance levels could be estimated in a relevant way by measuring the tolerance of periphyton photosynthesis in a short-term test system. These findings show that the basic requirements for the use of induced tolerance as an ecotoxicological tool at the community level are met. The rationale and potential applications of the pollution-induced community tolerance (PICT) concept are further outlined in Blanck et al. (1988).

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Ontogenetic Changes in the Distribution of Larval and Juvenile Yellow Perch (*Perca flavescens*): A Response to Prey or Predators?

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Post, J. R., and D. J. McQueen. 1988. Ontogenetic changes in the distribution of larval and juvenile yellow perch (*Perca flavescens*): a response to prey or predators? Can. J. Fish. Aquat. Sci. 45: 1820–1826.

Distribution of larval and juvenile yellow perch (*Perca flavescens*) in Lake St. George, Ontario, changed during development as follows: (1) early in development, the larvae were distributed exclusively offshore, both day and night; (2) larger larvae and juveniles migrated nearshore to offshore at dusk, returning the the nearshore zone at dawn; (3) the extent of this migration weakened as the fish grew, and they spent a greater porportion of their time nearshore and did not migrate as far at night; and (4) by the time juveniles reached approximately 30 mm total length, they were distributed exclusively in the nearshore habitat both day and night. Analysis of published reports on distribution patterns of larval and juvenile yellow perch and the European perch (*Perca fluviatilis*) suggests that the ontogenetic distribution patterns observed in Lake St. George are typical for the two *Perca* species. This regularity amongst lakes in ontogenetic distribution pattern occurred despite variation in the selective forces of prey and predator abundance in nearshore and offshore habitats. We conclude that the changes in distribution throughout early development are not in response to the proximate selective forces of prey abundance or predation risk

Au cours du développement, la répartition des larves et des juvéniles de la perchaude (*Perca flavescens*) dans le lac St. George (Ontario) a été modifiée de la façon suivante : 1) au début du développement, les larves se trouvaient exclusivement au large, tant le jour que la nuit; 2) des larves de plus grande taille et des juvéniles migraient vers le large au crépuscule, pour revenir vers le littoral à l'aube; 3) l'ampleur de la migration diminuait à mesure que les poissons se développaient, et ils passaient une plus grande partie de leur temps près du littoral et migraient moins loin la nuit; 4) lorsque les juvéniles atteignaient une longueur totale d'environ 30 mm, ils fréquentaient la zone littorale le jour que la nuit. L'analyse des rapports publiés sur les profils de répartition des larves et des juvéniles de perchaude et de *Perca fluviatilis* semble indiquer que les profils de répartition ontogénique observés dans le lac St. George sont caractéristiques des deux espèces de *Perca*. Cette régularité du profil de distribution ontogénique d'un lac à l'autre existe malgré la variation des forces de sélection de l'abondance des proies et des prédateurs dans les habitats côtiers et hauturiers. Nous concluons que les modifications de la répartition au début du développement ne s'effectuent pas en réponse aux forces proximales de sélection de l'abondance des proies ni du risque de prédation.

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Larval and juvenile stages of yellow perch (*Perca flavescens*) and the closely related European perch (*Perca fluviatilis*) typically (1) hatch 10–20 d after spawning from egg masses laid in the littoral zone, (2) remain in the littoral zone until the yolk sac is absorbed, approximately 1–2 wk, (3) migrate to the pelagic zone for approximately 4–8 wk, and (4) migrate back to the littoral zone or to the demersal zone for the remainder of the season. Kelso and Ward (1977) suggested that the offshore migration by larval yellow perch in West Blue Lake allowed utilization of the abundant small-bodied prey to maximize growth rates. They suggested that the return to the littoral zone is a predator avoidance mechanism, in response to predation by pelagically feeding walleye (*Stizostedion vitreum vitreum*). In addition, they suggested that observed diel vertical migration of the perch during the pelagic phase is probably also a response to predation risk. In contrast, Whiteside et al. (1985) suggested that the offshore migration of larval perch in Lake Itasca, Minnesota, is a predator avoidance response to the abundant littoral zone predators. Since their sampling was only after dark, diel patterns were not observed. They also suggested that returning to the littoral zone, after several weeks offshore, is in response to a decrease in limnetic zooplankton abundance and more abundant and larger potential prey in the littoral zone.

Here we describe both diel distribution and the ontogenetic change in distribution during the transition from pelagic to littoral zones for larval and juvenile yellow perch in Lake St. George, Ontario. Two hypotheses were tested: (1) that migrations are related to feeding periodicity and to the spatial distribution of prey and (2) that migrations are in response to predation risk. The detailed data collected in Lake St. George as well as published literature on early life history of *Perca* sp. are used to address the stated hypotheses.

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Materials and Methods

Larval and juvenile yellow perch and zooplankton were sampled in Lake St. George, Ontario (43°57′N, 79°25′W), in the spring of 1982. Lake St. George is a 10.4-ha kettle lake situated on the Oak Ridges Moraine northeast of Toronto, Ontario. The lake is dimictic, has a clinograde oxygen profile, a mean depth of 5.7 m, and a maximum depth of 15.0 m. The dominant species of the fish community in 1982 were yellow perch, bluegill (*Lepomis macrochirus*), golden shiner (*Notemegonus crysoleucas*), largemouth bass (*Micropterus salmoides*), and northern pike (*Esox lucius*). The sampling gear used for collecting both young yellow perch and zooplankton consisted of two fiberglass Miller samplers (Miller 1961) mounted horizontally at the end of a 5.08-cm outside diameter steel pole held vertically by a frame at the bow of a 6-m boat, powered by a 25-hp outboard motor. The sampling depth could be adjusted from 0.5 to 3.5 m by lowering the pole into the water vertically. The samplers had a mouth diameter of 10.5 cm; one was fitted with a 500-μm net and bucket for catching young fish and the other with a 150-μm net and bucket for capturing zooplankton. A calibrated General Oceanics flowmeter was attached to the pole to allow calculation of volume sasmpled. A constant tow speed of 3.5 $m \cdot s^{-1}$ was maintained with a speedometer for all tows of 0.5 and 1.5 m depth. Deeper tows necessitated a reduction in speed to 1.7 $m \cdot s^{-1}$.

The surface waters of Lake St. George were sampled at approximately 3-h intervals on four 24-h periods (May 20, May 27, June 3, and June 10) throughout the 4-wk period that larval and juvenile perch were distributed in the open water, before their migration to the littoral zone. A single daytime series of samples were collected on intermediate dates (May 24, May 27, and June 3). We caught no yellow perch in the pelagic zone before or after this 4-wk period. Fish and zooplankton samples were preserved in 95% ethanol for analysis at a later date. The standard tow sites were (1) nearshore at 0.5 m depth over the 1.5-m contour, (2) midlake at 0.5 m depth over the 6.0- to 7.0-m contour, (3) midlake at 1.5 m depth over the 6.0- to 7.0-m contour, (4) offshore at 0.5 m depth over the 9.0- to 11.0-m depth contour, and (5) offshore at 1.5 m depth over the 9.0- to 11.0-m contour. Each tow consisted of a total circuit of the lake for nearshore and midlake zones and two circuits of the lake for the offshore zone. Tows were 3–5 min in duration. Diel changes in horizontal distribution were determined by combining the data from the 0.5- and 1.5-m tows. A series of deeper tows (2.5 and 3.5 m) were done at midday and midnight on June 3 to test the hypothesis that some part of the population was missed by the standard sampling. The relative proportion of perch in each stratum was calculated from catches for each eight or nine sampling periods throughout each 24-h experiment. To estimate the number of yellow perch in each stratum, the density per litre was multiplied by the volume of the stratum. The relative proportion in each stratum was calculated as a proportion of the sum of the estimates for all strata. Therefore, relative proportion represents the proportion of the total estimated population that is in a particular stratum.

To determine feeding periodicity, five perch were selected randomly from the fish collected from the stratum containing the greatest proportion of the population for each 3-h sampling interval. Whole gastrointestinal tracts were dissected out, blotted dry, and weighed to the nearest 0.1 mg. A regression equation, relating body weight (BW, grams) to the weight of an empty gastrointestinal tract (GIW, grams), was determined from all empty guts observed:

$$\ln \text{GIW} = 1.08 \ln \text{BW} - 2.48 \quad (r^2 = 0.99, N = 46).$$

The weight of food was calculated by subtracting the predicted weight of an empty gastrointestinal tract from the observed weight. Feeding periodicity was expressed as the change in the ratio of food weight to body weight throughout each 24-h period.

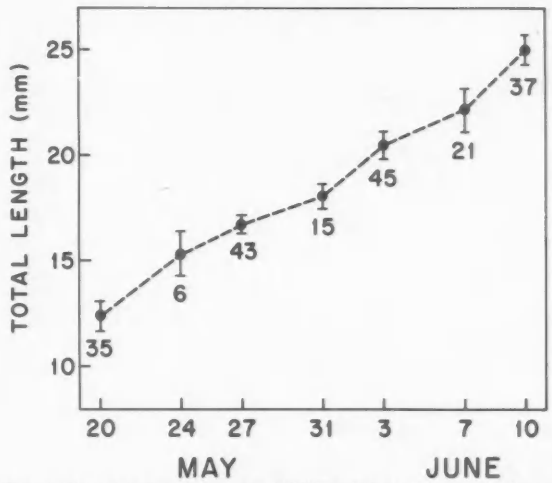

FIG. 1. Growth in length (mean and 95% confidence intervals) of larval and juvenile yellow perch in Lake St. George. Sample size is indicated.

A diet description was determined from the mean stomach contents of five fish sampled at random from the catch at the dusk peak feeding interval. For comparison with food availability, pre-dusk and post-dusk plankton samples collected in the 150-μm-mesh Miller sampler were analyzed for both the nearshore and offshore zones. The offshore samples were made up of equal subsamples from the midlake and offshore tows at both depths.

Zooplankton from stomach samples and lake samples were processed identically: they were identified, enumerated, and measured using a semiautomated system similar to that described by Sprules et al. (1981). Subsamples containing 300–500 organisms were randomly taken from the samples. Organisms were magnified by approximately 28× using a video camera and monitor connected to a stereo dissecting microscope. Measurements were made from the monitor using a caliper-mounted potentiometer interfaced to a microcomputer through an analog to digital converter. The digital signal was calibrated to real length and the data were stored on floppy disk. Taxonomic identification was to family for Cladocera: Chydoridae, Daphnidae, Sididae, and Bosminidae and to suborder for the subclass Copepoda:Cyclopoida and Calanoida, and individuals of the phylum Rotifera were counted as a single group with the exception of *Asplachna* sp. which was counted separately. The data were summarized into 0.1-mm length classes and number per litre calculated for each taxonomic category.

Results

Distribution Pattern

On May 20 when the yellow perch averaged 12.7 mm total length (TL) (Fig. 1), they were distributed almost exclusively

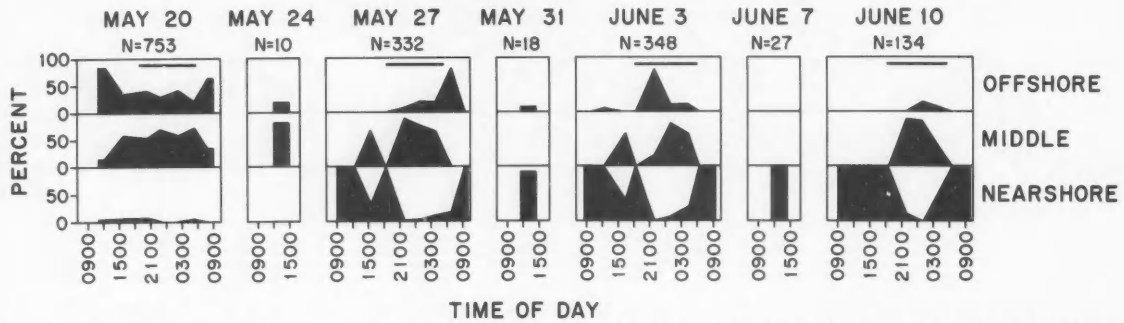

FIG. 2. Horizontal distribution of the larval and juvenile yellow perch in Lake St. George during four 24-h diel trawl experiments and for single midday trawl series on the intervening dates.

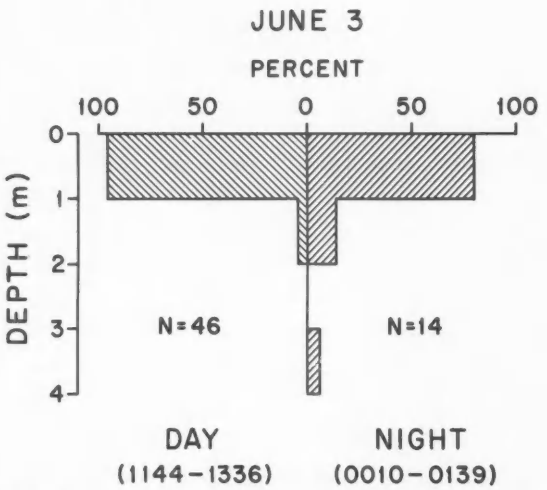

FIG. 3. Day and night depth distribution of larval and juvenile yellow perch in Lake St. George on June 3.

TABLE 1. Analysis of variance of the abundance of young-of-the-year yellow perch during the day and night in the nearshore, midlake, and offshore strata in Lake St. George. Significant results ($p < 0.05$) are indicated by an asterisk.

	May 20		May 27		June 3		June 10	
	df	*F*	df	*F*	df	*F*	df	*F*
Main effects								
Time	1	9.67*	1	2.15	1	1.17	1	0.00
Strata	2	12.52*	2	1.11	2	0.72	2	3.79*
Interaction								
Time × strata	2	7.06*	2	4.21*	2	3.63*	2	3.86*

in the midlake and offshore zones both day and night (Fig. 2). The daytime series on May 24 suggests the same pattern. The pattern had changed by May 27. During daylight hours the majority of the cohort was distributed in the nearshore zone, migrating to the midlake and offshore zones at approximately dusk and returning at approximately dawn. This pattern was very similar on June 3 and its corroborated by the midday series on May 31. There appears to be a short-term offshore migration and return in midafternoon which is of approximately equal timming and magnitude on both May 27 and June 3. By June 7 and June 10 the yellow perch were exclusively nearshore during daylight hours, leaving the nearshore zone at dusk and returning at dawn. The majority of the population moved only as far as the midlake zone rather than to the offshore zone as observed previously. On June 14 and June 20, yellow perch were not caught with the Miller sampler despite repeated visual observations of their occurrence in the nearshore zone both day and night. Limited day and night beach seining on June 24 shows that nearshore catch per unit effort does not decrease at night, suggesting that the diel offshore migration has ceased before the yellow perch reach a mean length of 34 mm TL on that date.

Additional depth distribution data were collected both day and night on June 3 to test the hypothesis that part of the cohort was distributed deeper in the water column and was therefore missed by the standard sampling design. Depth distribution data suggest that the majority of the cohort was distributed in the upper 2.0 m of the water column both day and night (Fig. 3), which is consistent with most published literature (Houde 1969; Noble 1972; Coles 1981).

The statistical significance of the distributional patterns presented in Fig. 2 was assessed with a two-way analysis of variance. The treatments were Time (day versus night) and Strata (nearshore, midlake, and offshore). The observations were volumetric estimates of abundance. The diel changes in distribution (Fig. 2) are significant ($p < 0.05$) on all dates, as evidenced by the interaction term of Time and Strata (Table 1). The Strata effect was significant on May 20 and June 10 when the nearshore and offshore zones, respectively, were avoided both day and night (Fig. 2). There is a significant Time effect only on May 20. Examination of the means and standard deviations of the abundance estimates suggests that mean abundance at night is consistently higher than during the day for all dates but that variance increases as the fish increase in length. This renders the Time effect nonsignificant for the later dates and suggests that visual gear avoidance is important during the day.

The ontogenetic changes in distribution of larval and juvenile yellow perch observed in Lake St. George can be summarized as the following: (1) early in development, larvae remain offshore day and night; (2) larger larvae and juveniles migrate from offshore to nearshore at dawn, returning at dusk; (3) this migration weakens as the fish grow, and they do not migrate as far at night; and (4) by the time they reach 25–34 mm TL, they are distributed exclusively in the nearshore habitat.

TABLE 2. Percent composition by number of prey taxa in stomachs of larval and juvenile yellow perch and mean number and SD of zooplankton per fish in Lake St. George.

Species	May 20	May 27	June 3	June 10
Daphnia	2.2	0.5	8.5	24.6
Bosmina	1.5	8.3	32.6	11.0
Chydorids	0.0	0.3	0.0	0.0
Diaphanosoma	0.0	0.5	1.9	11.2
Cyclopoids	62.5	64.2	53.2	51.9
Diaptomus	0.0	0.0	2.8	1.0
Nauplii	3.7	1.1	0.6	0.0
Rotifers	30.2	25.1	0.6	0.0
Mean $N \cdot fish^{-1}$	27.2	74.8	108.0	105.6
SD	10.8	8.6	82.4	29.9

TABLE 3. Density (no.$\cdot L^{-1}$) of major prey organisms in nearshore (NS) and offshore (OS) habitats pre- and post-dusk.

	May 20		May 27		June 3		June 10	
	NS	OS	NS	OS	NS	OS	NS	OS
Pre-dusk								
Daphnia	18	18	0	46	9	66	23	74
Bosmina	104	66	48	76	162	75	188	118
Cyclopoids	34	18	2	3	3	12	5	24
Rotifers	2	1	1	1	0	1	1	1
Post-dusk								
Daphnia	47	60	5	37	22	82	51	82
Bosmina	150	132	422	166	233	202	363	203
Cyclopoids	51	35	22	11	10	11	11	11
Rotifers	1	2	2	2	1	0	0	0

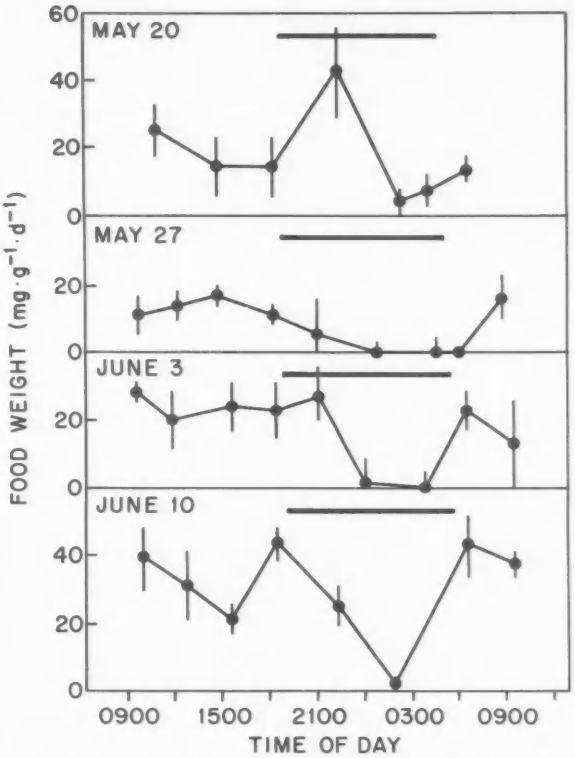

FIG. 4. Food weight in the intestinal tract of larval and juvenile yellow perch at approximately 3-h intervals throughout four 24-h experiments in Lake St. George. Hours of darkness indicated by horizontal bar.

Feeding Periodicity and Selectivity

Two general observations emerge from an analysis of feeding patterns (Fig. 4): (1) feeding intensity of larval yellow perch on May 20, when they were distributed offshore both day and night, was greatest during hours of darkness and (2) older larvae and juveniles (May 27 to June 10) fed during daylight hours and typically had dawn and dusk feeding peaks which were concurrent with the observed dusk offshore and dawn nearshore migrations.

This suggests the possibility that the migrations were in response to preferred quality or quantity of prey in the offshore zone. Stomach analyses of perch selected from periods of peak stomach fullness were used to assess the taxonomic composition of larval and juvenile perch prey (Table 2). Cyclopoids were numerically the most abundant prey for all sizes of perch examined. Rotifers were an important component of the diet of the smallest perch, but were reduced in importance as the perch grew larger. *Bosmina* sp. were most important at intermediate sizes of perch, and *Daphnia* sp. increased in importance with increasing perch size. The changing taxonomic composition in stomach samples parallels a shift to larger bodied prey as the larvae and juveniles grew.

We tested the hypothesis that the migration patterns are related to the density of preferred prey with lake zooplankton data (Table 3). The zooplankton samples, collected with Miller samplers with 150-μm mesh, underrepresented the rotifers. The rotifers that were collected were the largest in the population, being mostly large *Keretella* sp. On May 20, when the perch were offshore both day and night, the highest densities of their preferred prey, cyclopoids, were nearshore. On May 27, when the perch migrated offshore at dusk, both cyclopoids and *Bosmina* sp. were more abundant nearshore post-dusk. On June 3, cyclopoid abundance was similar nearshore and offshore post-dusk, *Bosmina* sp. abundance was higher nearshore post-dusk, and *Daphnia* sp. abundance was higher offshore both pre- and post-dusk. On June 10, cyclopoid density was similar nearshore and offshore post-dusk, *Bosmina* sp. abundance was highest nearshore post-dusk, and *Daphnia* sp. abundance was highest offshore both pre- and post-dusk. This suggests the possibility that the offshore migration is in response to higher *Daphnia* sp. densities in the offshore zone, at least on the later two sampling dates.

Since the rapidly growing perch selected the larger prey taxa, it is possible that the offshore zone provided larger prey organisms than the nearshore zone. A summary of the size distributions of prey in the perch stomachs and the size distributions of important prey (>5% by number) that occurred in the lake suggests that the observed migration patterns may have been influenced by the availability of preferred prey sizes (Fig. 5). On May 20, the prey size distributions indicate that the perch selected prey that were smaller, on average, than the prey available in any zone or time period. The size frequency plots also show the inadequate sampling of the Rotifera <0.2 mm. On May 27, prey >0.4 mm made up 36% of the stomach contents but were 6% or less of nearshore plankton communities whereas in the offshore post-dusk plankton, 39% were >0.4 mm. The pattern was more obvious on June 3 and June 10 when the perch

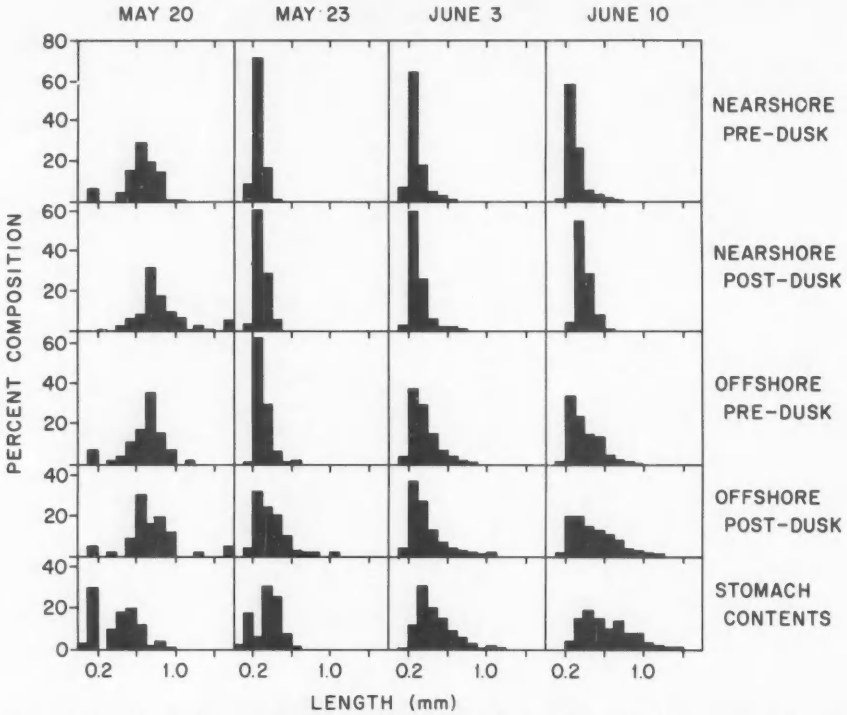

FIG. 5. Pre- and post-dusk zooplankton size distributions in the nearshore and offshore zones and larval and juvenile perch stomach content size distributions in Lake St. George.

were selecting sizes that were on average larger than the average available in the lake. On June 3, 57% of the prey organisms were >0.4 mm and only 9–11% of the nearshore pre- and post-dusk samples were in these size classes. On June 10, 62% of the prey organisms were >0.5 mm and only 7–10% of the nearshore pre- and post-dusk were in those size classes. The largest 23% of the length frequency distribution of the diet was not represented at all in the nearshore zone samples.

Predators

In Lake St. George, the predator community is composed primarily of adult perch, northern pike, and largemouth bass (Post and Prankevicius 1987) which are primarily nearshore predators. The initial offshore migration after hatch could have been a response to the abundant nearshore predators, but the observed diel nearshore–offshore migrations increased the exposure of the juvenile perch to predators. Juvenile perch were distributed nearshore during the day, where they were most vulnerable to diurnally feeding predators.

Discussion

A general pattern of ontogenetic change in distribution of larval and juvenile yellow perch from lakes of diverse morphology, productivity, and predator species can be determined from a combination of this and other published studies (Table 4). The European perch exhibits the same patterns. The first observation common to all studies is that there is always a period in early life history during which larval perch are distributed offshore. This occurs in situations where there are abundant offshore predators such as the walleye in West Blue Lake (Kelso and Ward 1977) and in Oneida Lake (Houde 1969; Noble 1972; Nielsen 1980) and in Lakes where predation pressure is primarily in the nearshore zone such as in Lake Opinicon (Amundrud et al. 1974; Keast 1985), Lake Itasca (Whiteside et al. 1985), and Lake St. George. This pattern has also been noted in other lakes where the spatial distribution of predation pressure is less well known (Faber 1967; Coles 1981; Cucin and Faber 1985).

The second observation is that the young of both species appear to leave the open water after a number of weeks. In Oneida Lake, which is relatively shallow, isothermal, and oxygenated to the bottom, some juveniles migrate to the bottom, while others migrate to the nearshore zone (Lin 1975). In Lake Itasca (Whiteside et al. 1985), Windermere (Guma's 1978), Llyn Tegid (Coles 1981), and Lake St. George, all of which thermally stratify, the juveniles migrate to the nearshore zone, avoiding the cold hypolimnetic water. In Lake St. George, demersal distribution is prevented by an anoxic hypolimnion. These observations, from a diverse set of lakes, suggest that after leaving the pelagic habitat, the juveniles select a habitat with sufficient light and temperature for foraging near the bottom. In stratified lakes, this means the nearshore habitat; in nonstratified lakes, this means both nearshore and demersal zones.

From the published literature, it is difficult to generalize about the timing of the migration away from the surface offshore habitat. Coles (1981) showed that the nearshore migration in Llyn Tegid was complete when the juvenile perch had reached 19 mm TL. He sampled only during the daytime, and

TABLE 4. Summary of the major literature findings on the spatial and temporal distribution patterns of larval and juvenile *Perca* spp. The size range of individuals captured during the study and the sampling gear employed are summarized. Sampling depth is reported as either surface or the range of depths sampled. Distance from shore is reported as nearshore (NS) to offshore (OS) or as distance in metres from the shore. Time sampled is day or night or both day and night. The observed spatial and temporal distribution of larvae and juveniles and prey and predators is summarized. Information not reported (NR) is noted.

Species	Lake	Size range (mm)	Gear	Depth (m)	Distance from shore (m)	Time	Notes	Reference
P. flavescens	Little John Erickson	NR	Conical tow net	Surface	50–200	Night	Larvae caught offshore	Faber 1967
P. flavescens	Oneida	10–18	Miller sampler	1–4	100–1000	Day	Abundance greater nearshore	Nobel 1968, 1972
P. flavescens	Oneida	6–9	Conical tow net	2–3	100–1000	Day/night	No day/night differences	Houde 1969
					2- to 5-m contour		No relationship to prey abundance, predators > offshore	
P. flavescens	Opinicon	6–11	Conical tow net	Surface	NS and OS	Night	Perch >11 mm not caught, predators > nearshore	Amundrud et al. 1974
P. flavescens	West Blue	5.6–>30	Conical tow net, sonar	All	NS and OS	Day/night	<30 mm offshore, >30 mm nearshore	Kelso and Ward 1977
P. fluviatilis	Windermere	6–90	Conical tow net, beach seine	Surface	NS to 600	NR	Offshore until 16 mm, nearshore >16 mm	Guma'a 1978
P. fluviatilis	Llyn Tegid	9–23	Miller sampler, purse seine, beach seine	Surface	NS to 400	Day	Offshore until 18 mm, nearshore >18 mm	Coles 1981
P. flavescens	Michigan	≤7.5	Conical tow net, benthic sled	0–20	6- to 20-m contour	Day/night	Offshore distribution throughout water column	Perrone et al. 1983
P. flavescens	Opeongo	5.8–18.5	Conical tow net	Surface	NS to 400	Day	Higher abundance offshore (8–12 mm), higher abundance nearshore (>12 mm)	Cucin and Faber 1985
P. flavescens	Itasca	8–40	Conical tow net	1–2	NS and OS	Night	8–23 mm primarily offshore, >23 mm primarily nearshore, prey abundance > nearshore, predator abundance > nearshore	Whiteside et al. 1985
P. flavescens	St. George	12–35	Miller sampler	0.5–3.5	NS and OS	Day/night	12 mm offshore, >25 mm nearshore, 17–25 mm diel migration, variable prey abundance, predators > nearshore	This study

if the diel pattern observed in Lake St. George is typical, nighttime sampling might have indicated that the migration was not yet complete. In Lake Itasca (Whiteside et al. 1985), sampling was conducted only at night, and 25 mm was noted as the juvenile total length at which the cohorts completed nearshore migration. Daytime sampling may have shown that the inshore migration began before the juvenile perch reached 25 mm TL. The offshore to demersal transition in Oneida Lake occurred one year at 25 mm TL and a second year at 44 mm TL (Lin 1975). The transition was not in response to more favourable prey abundance, or reduced predation risk, but was correlated with avoidance of high surface water temperature (Lin 1975). Gear avoidance, by the increasingly agile juvenile perch, can make it difficult to determine mean length accurately at time of migration. For instance, in Lake Opeongo, juvenile perch were not caught either nearshore or offshore at lengths greater than 18.5 mm (Cucin and Faber 1985). In Lake Opinicon, larval perch were not caught at lengths greater than 11 mm in the offshore zone (Amundrud et al. 1974). Therefore, both time of sampling and gear avoidance can lead to the inappropriate conclusions about when the change from offshore to nearshore distribution begins and when it is complete.

Three potential explanations for the migration to the nearshore habitat have been suggested. The first, suggested by Kelso and Ward (1977), was that with the development of pigmentation, the juvenile perch would be more susceptible to predation by walleye in the offshore habitat, and therefore, nearshore migration to vegetative cover would provide a refuge. In contrast, the primary predation risk in Lake St. George is in the nearshore zone, and yet the juveniles make the same offshore to nearshore migration as described by Kelso and Ward (1977). Another explanation, suggested by Whiteside et al. (1985), is

that the nearshore migration is in response to greater nearshore prey abundance. This is not the case in Lake St. George where the nearshore habitat has fewer and smaller zooplankton prey at a time when the juvenile perch are selecting the largest zooplankters available. Larger benthic invertebrates are available in the nearshore and demersal habitat but they are not an important prey item for juvenile perch of the size that make the migration to nearshore or demersal habitats (Lin 1975; Kelso and Ward 1977; Guma'a 1978; this study). A third hypothesis has been suggested by Schneider (1923, cited in Coles 1981) who ascribed the inshore migration to behavioural thermoregulation, in response to the warmer nearshore waters. This may be a factor in large lakes, but in smaller lakes such as Lake St. George, there is no consistent difference between offshore epilimnetic and littoral zone temperatures.

The diel horizontal migrations observed in Lake St. George have not been observed in other lakes. It may be due to the restricted sampling times used by other investigators (Faber 1967; Amundrud et al. 1974; Coles 1981; Whiteside et al. 1985) or to the greater horizontal distances involved in larger lakes. The horizontal displacement observed in Lake St. George was 100–200 m. In Llyn Tegid, the juvenile perch had to migrate 400–500 m offshore to be captured at Coles' (1981) offshore stations. Whiteside et al. (1985) did not include information on the spatial distribution of their sampling sites, but because they sampled only at night, it is possible that the perch exhibited the same diet patterns as in Lake St. George. The largest sizes caught offshore at night in Lakes Itasca and St. George were similar. Kelso and Ward (1977) showed that offshore catches of larval and juvenile perch were higher at night than during the day, but it is unclear whether this is caused by gear avoidance or migration to the offshore zone. The horizontal distances involved in a nearshore–offshore dusk migration in West Blue Lake were at least several hundred metres.

The observed regularity in the pattern of ontogenetic changes in distribution of larval and juvenile *Perca* sp. amongst a diverse set of lakes suggests that there is a significant genetic component to the behaviours. This regularity persists despite the conflicting selective forces of prey and predator abundance in nearshore and offshore habitats that differ substantially between the lakes studied. The timing of the major early life history migrations may be flexible betwen and within populations, but current knowledge is inadequate to address this fully.

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Effets chimiques et cytologiques de la contamination expérimentale de l'huître *Crassostrea gigas* Thunberg par l'argent administré sous forme dissoute et par voie alimentaire

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L'exposition de jeunes huîtres (*Crassostrea gigas* Thunberg) à l'Ag dissous dans l'eau (20 $\mu g \cdot L^{-1}$) ou incorporé à du phytoplancton (59,7 $\mu g \cdot g^{-1}$), provoque une bioaccumulation du métal qui atteint un pallier dès ou avant le quatorzième jour. La contamination ne cause aucune lésion cytologique, mais elle amplifie l'émission des spermatozoïdes et diminue le stockage du glycogène dans le tissu vésiculeux. Des Ag-protéines, naturellement présentes chez les témoins où elles fixent 55 % du métal, complexent 30 % de l'Ag des huîtres contaminées. Le stockage du métal dans les lysosomes des cellules des branchies et du système digestif est très faible ; la plus grande partie est immobilisée sous forme de sulfure dans les amoebocytes et dans les lames basales. Le pallier de concentration peut être imputé à l'élimination continue des amoebocytes. Du point de vue écotoxicologique, l'immobilisation d'Ag sous forme de sulfure indique qu'une fraction importante du polluant (environ 70 %) ne peut être transférée aux niveaux trophiques supérieurs.

The exposure of young oysters (*Crassostrea gigas* Thunberg) to Ag introduced into seawater (20 $\mu g \cdot L^{-1}$) or linked to phytoplankton (59.7 $\mu g \cdot g^{-1}$) is responsible for a bioaccumulation of this metal, the level of which reaches a plateau within 14 d. This contamination does not induce any cytological lesion, but it leads to an enhancement of the emission of spermatozoons and a decrease of the storage of glycogen in the interstitial tissue. Ag-proteins (present by nature in oysters) account for 30% of the metal in contaminated oysters (55% in controls). The metal storage in the lysosomes of branchial and digestive cells is poor whereas the major part is sequestered as Ag-sulphide in amoebocytes and basement membranes. The steady state observed after 2 wk of exposure may be due to the continuous elimination of amoebocytes. From an ecotoxicological point of view, the transfer of Ag to higher trophic levels will be limited, since an important fraction (70%) of the metal is sequestered in a very stable physicochemical form.

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L'argent donne lieu à des pollutions locales fréquentes. Au métal naturel provenant du lessivage des sols s'ajoute une fraction liée aux activités industrielles (combustion de déchets urbains, corrosions) et surtout à l'industrie photographique. L'extension géographique de cette pollution est bien mise en évidence par Bryan *et al.* (1983) qui montrent que, sur 59 estuaires de Grande-Bretagne, 21 sont contaminés. De plus, de l'Ag 110 m est produit et rejeté dans les milieux aquatiques au cours de plusieurs étapes du cycle du combustible nucléaire. Les études expérimentales montrent que l'Ag est très toxique pour les larves de divers Invertébrés dont les Mollusques (Amiard 1976 ; Calabrese *et al.* 1977). En revanche, les individus ayant dépassé le stade larvaire supportent des expositions prolongées en même temps qu'ils accumulent des quantités importantes du métal (Pouvreau et Amiard 1974). Il en est de même dans les estuaires pollués (Bryan et al. 1983).

Les mécanismes physiologiques responsables de la résistance des mollusques et de leur capacité d'accumulation sont encore incomplètement connus. Chez la Scrobiculaire, la radioactivité maximale des tissus mous est atteinte relativement

vite (1 mo) après contamination par les formes solubles de l'Ag 110 m, alors que la nourriture intervient pour une faible part (Amiard 1978a, 1979a, 1979b) ; au niveau histologique, ce sont la glande digestive et le manteau qui concentrent le plus le métal (Amiard 1978b, 1978c). Chez l'Huître *Ostrea sinuata*, l'accumulation a lieu surtout dans la masse viscérale, en particulier dans le coeur (Brooks et Rumsby 1965). Chez la Moule, la capture du métal par une protéine de type métallothionéine, envisagée par Marshall et Talbot (1979), est désormais démontrée ; il s'agit d'une protéine complexant à la fois l'Ag et le Cu (George *et al.* 1986). De plus, le métal est complexé par des protéines de poids moléculaire élevé, et, comme chez la crépidule, il se dépose dans les lames basales (Nelson *et al.* 1983 ; George *et al.* 1986). Selon ces derniers auteurs, le métal immobilisé dans ces structures est lié aux groupements thiols des glycoprotéines et aux groupes sulfates de mucopolysaccharides. Enfin, les glandes péricardiales et les macrophages participent également au stockage.

L'importance relative des divers modes de contamination, l'évolution dans le temps des concentrations en Ag des mollusques, l'accumulation dans des cellules autres que celles précédemment citées, la recherche d'éventuelles lésions et effets métaboliques restent à envisager. Il est également intéressant de déterminer si les mécanismes de complexation moléculaire et de stockage décrits chez la Moule s'appliquent à d'autres espèces. Nous avons donc choisi comme matériel d'étude l'Huître *Crassostrea gigas*, en raison de sa fréquence dans les estuaires, de son intérêt économique et de sa capacité de détoxifier des métaux des groupes IB et IIB (Cu, Cd) (Amiard *et al.* 1986 ; Engel et Brouwer 1982 ; Fowler *et al.* 1986 ; Jeantet *et al.* 1985 ; Martoja et Martin 1985). De plus l'Huître, à l'inverse d'autres mollusques, n'est pas un concentrateur d'Ag naturel. En effet, les teneurs en Ag des tissus mous n'excèdent pas 7 $\mu g \cdot g^{-1}$ (voir Eisler 1981 ; Boehm *et al.* 1987) et le métal est indécelable dans les cellules à pores qui, chez les concentrateurs d'Ag, l'accumulent sous forme de sulfure (Martoja *et al.* 1985).

Matériel et méthodes

Conditions d'élevage et de contamination — Prélèvements

De jeunes huîtres âgées de 10 mo après l'éclosion ont été réparties en trois groupes et exposées pendant 4 sem à l'Ag introduit en surcharge dans l'eau de mer et/ou associé à la nourriture phytoplanctonique (Diatomée : *Skeletonema costatum*). Un groupe témoin était constitué concomitamment (schéma 1).

Les algues ont été cultivées en grand volume (800 L) dans une eau de mer souterraine, naturellement enrichie en sels nutritifs selon la méthode préconisée par Dréno (1983). Elles ont été contaminées par l'Ag, en solution nitrique, à raison de 20 $\mu g \cdot L^{-1}$ au premier et au troisième jour de la culture. La concentration de la solution mère a été choisie pour que la quantité d'acide nitrique introduite dans le milieu (0,16 mL·800 L^{-1}) n'entraîne pas de diminution du pH. Après 4 d, les algues (contaminées et témoins) ont été concentrées, rincées à l'eau de mer normale, concentrées à nouveau et cette eau de mer chargée d'algues a été congelée rapidement par l'azote liquide en nombreux lots de petit volume. Des fractions aliquotes de la suspension de diatomées ont été prélevées sur plusieurs lots de nourriture afin de déterminer la biomasse par unité de volume et la concentration de l'Ag dans le phytoplancton témoin ou contaminé. Les lots de nourriture congelée ont ensuite été décongelés successivement à température ambiante pour fournir quotidiennement deux rations de nourriture aux huîtres. Chacune de ces rations représentait environ 1 % du poids des tissus mous de l'animal. Elle n'entraînait pas la production de pseudofaeces. Ce protocole permet de distribuer tout au long de l'expérience des rations qualitativement et quantitativement

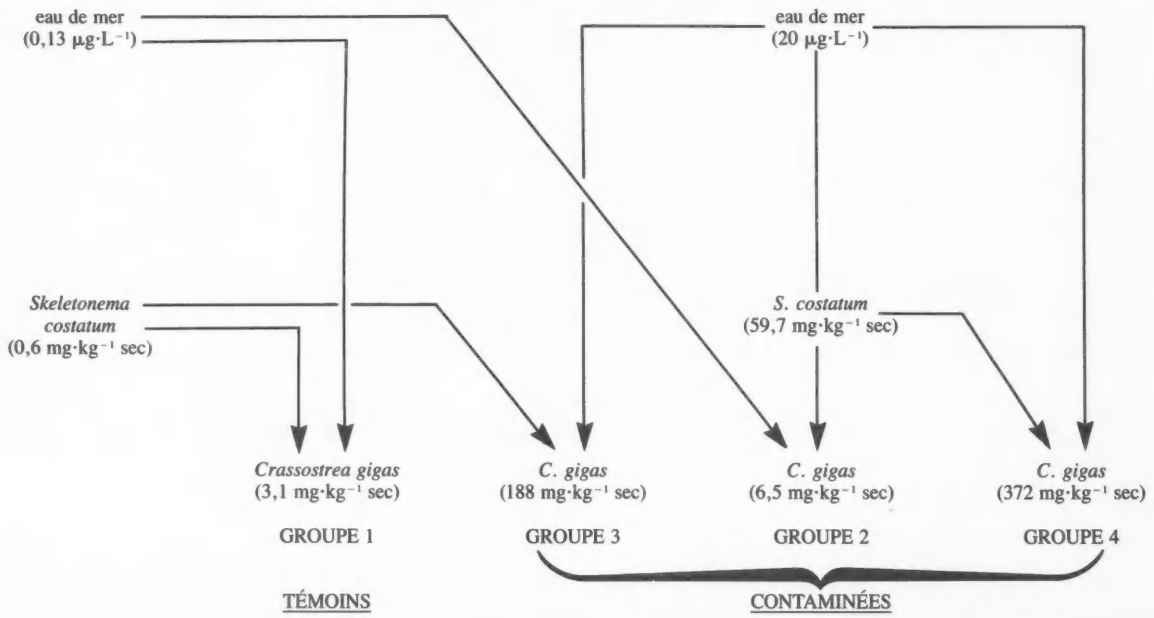

SCHÉMA 1. Influence de la voie de contamination sur la teneur en Ag des huîtres à la fin de l'expérience.

identiques et de disposer d'algues rincées qui ne libèrent pas l'Ag dans l'eau, ce qui permet de différencier parfaitement les sources de contamination (eau ou nourriture). En contrepartie, il n'est pas possible d'assurer une alimentation des huîtres en régime continu.

L'expérience de contamination des huîtres a été réalisée en mai 1985 dans les conditions naturelles prévalant en cette saison dans la zone ostréicole de la baie de Bourgneuf. L'eau de mer était prélevée dans les claires[1], mise à sédimenter en bassin de 50 m^3 couvert d'une ombrière pour éviter les développements d'algues et filtrée à 1 μm. Pour les groupes d'huîtres soumis à la contamination par l'eau, 20 $\mu g\ Ag \cdot L^{-1}$ étaient introduits sous forme ionique en solution dans l'acide nitrique à 1 %. À cette concentration, inférieure à la solubilité du nitrate d'argent en solution saline, la totalité de l'Ag introduit est sous forme dissoute dans le milieu. Vingt-quatre heures après la contamination, en moyenne 59 % de la surcharge initiale restaient dans la phase aqueuse. Une expérience de contrôle effectuée dans des aquariums ne contenant pas de mollusques a montré que la fixation sur les parois et sur les diffuseurs d'air ne représentait que 5 % du métal ajouté au milieu. Les principales causes de la décroissance de la concentration de l'Ag dans l'eau sont donc son assimilation par les huîtres ou son adsorption sur leurs coquilles. Bien que cette décroissance s'atténue ultérieurement, l'eau de mer contaminée a été renouvelée quotidiennement pour les groupes 3 et 4.

Les huîtres ont été introduites dans les milieux à raison d'un individu par litre d'eau de mer. Le poids frais moyen initial des tissus mous de chaque huître était voisin de 1 g. Après 2, 3 et 4 sem d'exposition, 10 huîtres ont été prélevées à partir de chaque groupe contaminé et du groupe témoin afin de déterminer la concentration d'Ag des tissus mous. Les investigations biochimiques et histologiques ont été menées chez des huîtres soumises au temps de contamination le plus long.

Techniques biochimiques

Tamisage moléculaire

Les huîtres ont été congelées pour la caractérisation des formes biochimiques de l'Ag. Les analyses ont porté individuellement sur deux huîtres témoins et quatre huîtres contaminées à partir de l'eau. Les parties molles des huîtres ont été broyées dans un potter à main dans 3 mL de tampon Tris 0,02 M, NaCl 0,15 M, pH 8,6. L'homogénat a été centrifugé 25 min à 30 000 × *g*. Pendant l'ensemble de ces opérations, les échantillons ont été maintenus à 4°C. Trois à quatre millilitres de surnageant ont été déposés sur une colonne de Sépharose CL 4 B (Pharmacia) (diamètre : 16 mm, hauteur 730 mm) équilibrée avec le tampon de broyage. L'élution à été effectuée avec le même tampon à un débit linéaire de 22 $cm \cdot h^{-1}$. Les constituants du mélange ont été repérés par leur absorbance à 280 nm. Les fractions collectées avaient un volume de 2,2 mL.

Caractérisation des fractions collectées après tamisage moléculaire

Les spectres d'absorption des fractions et leurs dérivés ont été déterminés à l'aide d'un spectrophotomètre Beckman DU-7. Le dosage des groupements thiols a été réalisé avec le réactif de Ellman selon la technique décrite par Tukendorf et Baszynski (1985). À 1 mL d'échantillon ont été ajoutés 0,45 mL de sodium dodécyl sulfate (SDS) (solution à 4 % dans un tampon Tris 0,1 M, pH 8,0) et 0,05 mL de 5,5′-dithiobis (2-acide nitrobenzoïque)(DTNB) (40 mg de DTNB dans 10 mL de tampon Tris 0,1 M, pH 8,0). La lecture de l'absorbance a été effectuée à 412 nm sur le spectrophotomètre Beckman DU-7. Après correction des absorbances non spécifiques dues aux différents réactifs, les calculs des concentrations molaires ont été réalisés en employant un coefficient d'extinction molaire de 13 600.

Dosage de l'Ag par spectrométrie d'absorption atomique

L'Ag a été dosé sur le phytoplancton, les tissus mous des huîtres *in toto* et les culots de centrifugation (voir ci-dessus) après séchage à 80°C pendant 24 h. La minéralisation et le dosage par spectrométrie d'absorption atomique électrothermique ont ensuite été réalisés selon la méthode d'Amiard *et al.* (1987) qui permet d'atteindre une limite de détection de 0,2 $\mu g \cdot kg^{-1}$ (poids sec). La concentration en Ag des diverses fractions collectées après tamisage moléculaire a été déterminée par la méthode des ajouts dosés après dilution de l'éluant (Tris) par de l'eau déminéralisée et de l'acide nitrique suprapur. De même, un dosage a été effectué sur une fraction aliquote avant tamisage moléculaire, afin de déterminer le pourcentage d'Ag récupéré après passage de l'échantillon sur la colonne.

Techniques microscopiques

Étude morphologique

La fixation des échantillons pour la microscopie photonique a été effectuée par le liquide de Carnoy (alcool absolu, chloroforme, acide acétique 6/3/1). Pour l'étude ultrastructurale, des fragments d'organes ont été fixés par le glutaraldéhyde à 3 % tamponné par du cacodylate de sodium 0,2 M, additionné de saccharose 0,35 M et post-fixés ou non par le tétroxyde d'osmium à 2 %. Le glutaraldéhyde pouvant produire des images artéfactuelles par réduction de complexes organiques d'Ag, les observations ultrastructurales ont également porté sur des coupes de pièces fixées au Carnoy. Les coupes à la paraffine, de 7 μm d'épaisseur, ont été colorées par le rouge solide-picro-indigocarmin ; les coupes ultrafines, de 100 nm, ont été observées sans renforcement de contraste ou après renforcement par l'uranyle-plomb.

Étude cytochimique

Le glycogène a été mis en évidence par la réaction à l'acide periodique-Schiff (APS) avec contrôle de digestion à l'amylase. Les groupements réducteurs ont été révélés par la réaction de Schmorl au ferricyanure ferrique (procédé au ferricyanure de potassium-perchlorure de fer), les groupements thiols par celle de Barrnett et Seligman au 2,2′-dihydroxy-6,6′-disulfure de dinaphtyle (DDD). L'identification des thiols a été contrôlée par blocage à la *N*-éthylmaléimide (voir Ganter et Jollès 1969).

Microanalyse élémentaire

La microanalyse a été effectuée par émission *X*, en dispersion de longueur d'onde, à l'aide d'une microsonde électronique Cameca MS 46 pour les coupes à la paraffine et d'une microsonde électronique Cameca MBX type Camebax pour les coupes ultrafines de matériel non osmié. Les cristaux des spectromètres suivants ont été utilisés : sur la microsonde MS 46, pentaerythritol (PET) pour le S, le Fe et l'Ag ; sur la microsonde Camebax, PET pour le Ca, le Cu et l'Ag, fluorure de

[1]Les claires sont des bassins littoraux d'une superficie faible (quelques centaines de m^2) et d'une profondeur réduite (environ 0,6 m) utilisées pour l'affinage des huîtres (engraissement accéléré et verdissement).

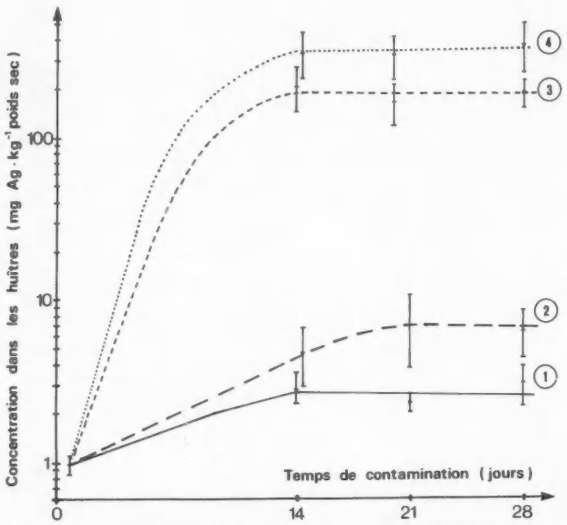

FIG. 1. Accumulation de l'Ag dans les tissus mous *in toto* des huîtres; 1) témoin ; 2) contamination par la nourriture ; 3) contamination par l'eau ; 4) contamination simultanée par l'eau et la nourriture. Le tracé de la courbe entre 0 et 14 d est hypothétique (concentrations moyennes affectées de l'intervalle de confiance à 95 %).

TABLEAU 1. Paramètres de la contamination expérimentale des huîtres par l'argent (groupe 2 : contamination par la nourriture seule; groupe 3 : contamination par l'eau seule; groupe 4 : contamination simultanée par l'eau et la nourriture) corrigés en tenant compte des quantités d'argent naturellement présentes dans l'eau, la nourriture et les huîtres témoins.

	Temps de contamination *t*		
	14 d	21 d	28 d
Quantité d'Ag (μg) accumulée par huître pendant le temps t			
Groupe 2	0,3	0,5	0,5
Groupe 3	29,7	16,7	18,4
Groupe 4	48,5	34,9	39,5
Surcharge d'Ag apportée par la nourriture contaminée (μg·huître⁻¹) pendant le temps t			
Groupes 2 et 4	1,8	2,7	3,7
Surcharge d'Ag disponible dans l'eau contaminée (μg·huître⁻¹) pendant le temps t			
Groupes 3 et 4	258	397	536
Pourcentage d'Ag accumulé par huître			
Groupe 2	17,9		
Groupe 3	11,5		
Groupe 4	18,6		

lithium (LiF) pour le Fe, le Ni, le Cu et le Zn, phtalate acide de thallium (TAP) pour l'Al et le P.

Tests de solubilité et de capture d'Ag

Afin de déterminer les caractères de solubilité de précipités situés dans les tissus des huîtres contaminées, des coupes à la paraffine et des coupes ultrafines ont été soumises, pendant 5

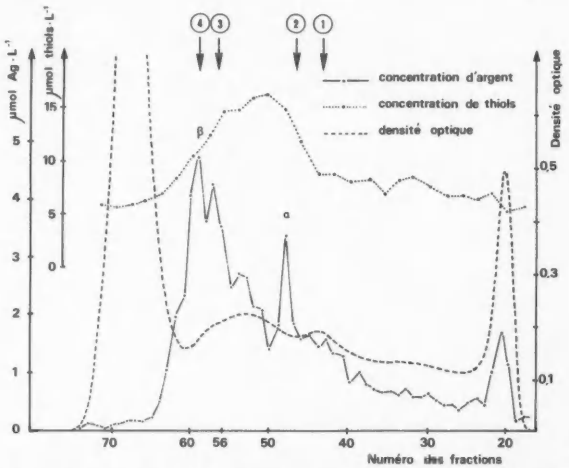

FIG. 2. Concentrations de l'Ag, des thiols et densité optique à 280 nm des différentes fractions séparées par tamisage moléculaire dans une huître contaminée à partir de l'eau pendant 28 d. La fraction 20 représente le pic d'exclusion, la fraction 68, le volume total. Fractions dans lesquelles avaient été élués les produits de référence lors de la calibration de la colonne : 1) ferritine (PM : 440 000) ; 2) catalase (PM : 232 000) ; 3) chymotrypsinogène (PM : 25 000) ; 4) ribonucléase (PM : 13 700).

à 60 min, à l'action d'acide nitrique 1 N, d'acide sulfurique 1 M, d'acide periodique à 1 % et de cyanure de potassium à 1 %. Les coupes à la paraffine ont ensuite été analysées à la microsonde, les coupes ultrafines observées au microscope électronique. Les possibilités de capture d'Ag par certaines structures histologiques ont été déterminées par immersion de coupes à la paraffine et de coupes ultrafines dans une solution à 5 % de nitrate d'argent éclairée par une vive lumière (technique de von Kossa). L'Ag a ensuite été recherché par la simple observation microscopique.

Résultats

Mortalité — Effets histologiques et métaboliques

Au cours des 4 sem d'expérimentation, aucune mortalité n'a été observée aussi bien chez les témoins que dans les trois groupes d'huîtres contaminées. Le poids des tissus mous (poids sec moyen initial : 136 mg) n'a varié significativement ni en fonction de la durée d'exposition, ni en fonction des conditions d'expérience (test *F* de Snedecor au niveau de probabilité de 99 %).

À l'examen histologique et cytologique, aucun organe ne présente de lésions, mais l'émission des spermatozoïdes dans les voies génitales est amplifiée. Les capacités de stockage des réserves glucidiques par les cellules du tissu vésiculeux sont diminuées. En effet, alors que le glycogène est abondant chez les témoins et chez les huîtres exposées à la contamination par voie alimentaire, le tissu vésiculeux en est très peu chargé ou dépourvu après contamination par l'eau ou par les deux voies.

Contamination des tissus mous *in toto*

Au cours des deux premières semaines, la concentration d'Ag augmente dans les tissus mous des huîtres des quatre groupes, puis se stabilise pendant les 2 sem suivantes (fig. 1). L'aug-

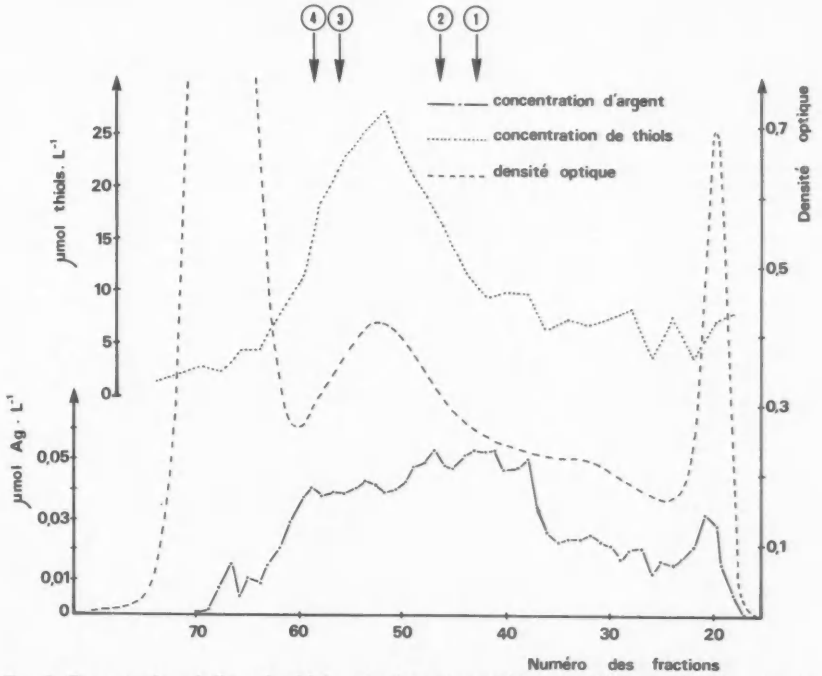

FIG. 3. Concentrations de l'Ag, des thiols et densité optique à 280 nm des différentes fractions séparées par tamisage moléculaire dans une huître témoin. Voir légende de la fig. 2.

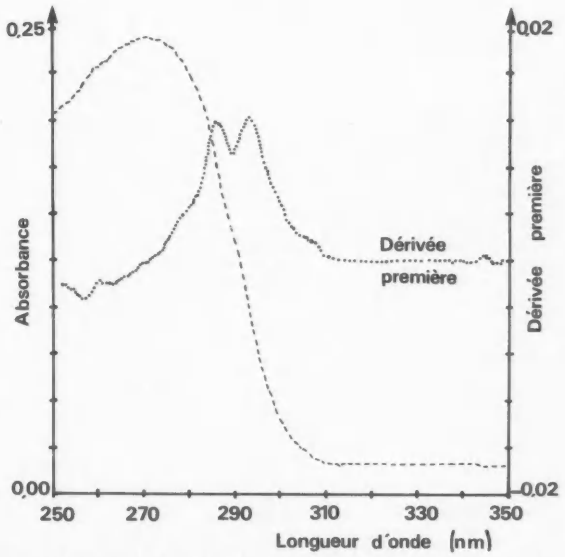

FIG. 4. Spectre de densité optique et dérivée première établis pour la fraction 56 (cf. fig. 2) isolée par tamisage moléculaire. Les résultats sont similaires pour les autres fractions correspondant aux pics d'argent α et β.

mentation observée chez les témoins pourrait être due à une modification des conditions d'élevage (entre autres le passage d'une nourriture naturelle plurispécifique à une nourriture contrôlée monospécifique) entraînant une adaptation du métabolisme des huîtres qui aboutit à un nouvel équilibre avec le milieu.

La consommation de nourriture contaminée induit une accumulation supplémentaire d'Ag, mais qui reste inférieure à celle produite par l'eau de mer polluée. La double voie de contamination induit les concentrations d'Ag les plus élevées (fig. 1).

Connaissant la quantité totale d'Ag de chaque huître pour chaque mode de contamination et chaque durée d'exposition, il est possible d'estimer la quantité d'Ag accumulée en moyenne par une huître contaminée pendant un temps donné (tableau 1). Elle est égale à la quantité moyenne d'Ag au temps t (14, 21 ou 28 d) diminuée de la quantité moyenne d'Ag d'une huître témoin. À partir des données sur la suspension de diatomées servant de nourriture (biomasse par unité de volume et concentration de l'Ag dans les algues), on peut estimer la quantité d'Ag reçue quotidiennement par voie alimentaire par chaque huître (1,33 ng pour les huîtres des groupes 1 et 3 ; 139 ng pour les huîtres des groupes 2 et 4). Comme précédemment, la surcharge d'Ag provenant de la nourriture contaminée est évaluée (tableau 1) en tenant compte des quantités naturellement présentes dans les diatomées témoins. La densité des huîtres étant d'un individu par litre, on peut admettre que la quantité d'Ag disponible quotidiennement par individu est égale à la quantité présente dans 1 L d'eau de mer (0,13 µg pour les huîtres des groupes 1 et 2 ; 20 µg pour les huîtres des groupes 3 et 4). Les surcharges disponibles pour les huîtres contaminées par l'eau sont calculées (tableau 1) en tenant compte des concentrations d'Ag dans l'eau de mer naturelle.

Connaissant les quantités d'Ag accumulées dans les huîtres pendant un temps donné, les quantités apportées par voie alimentaire et les quantités disponibles dans l'eau pendant le même

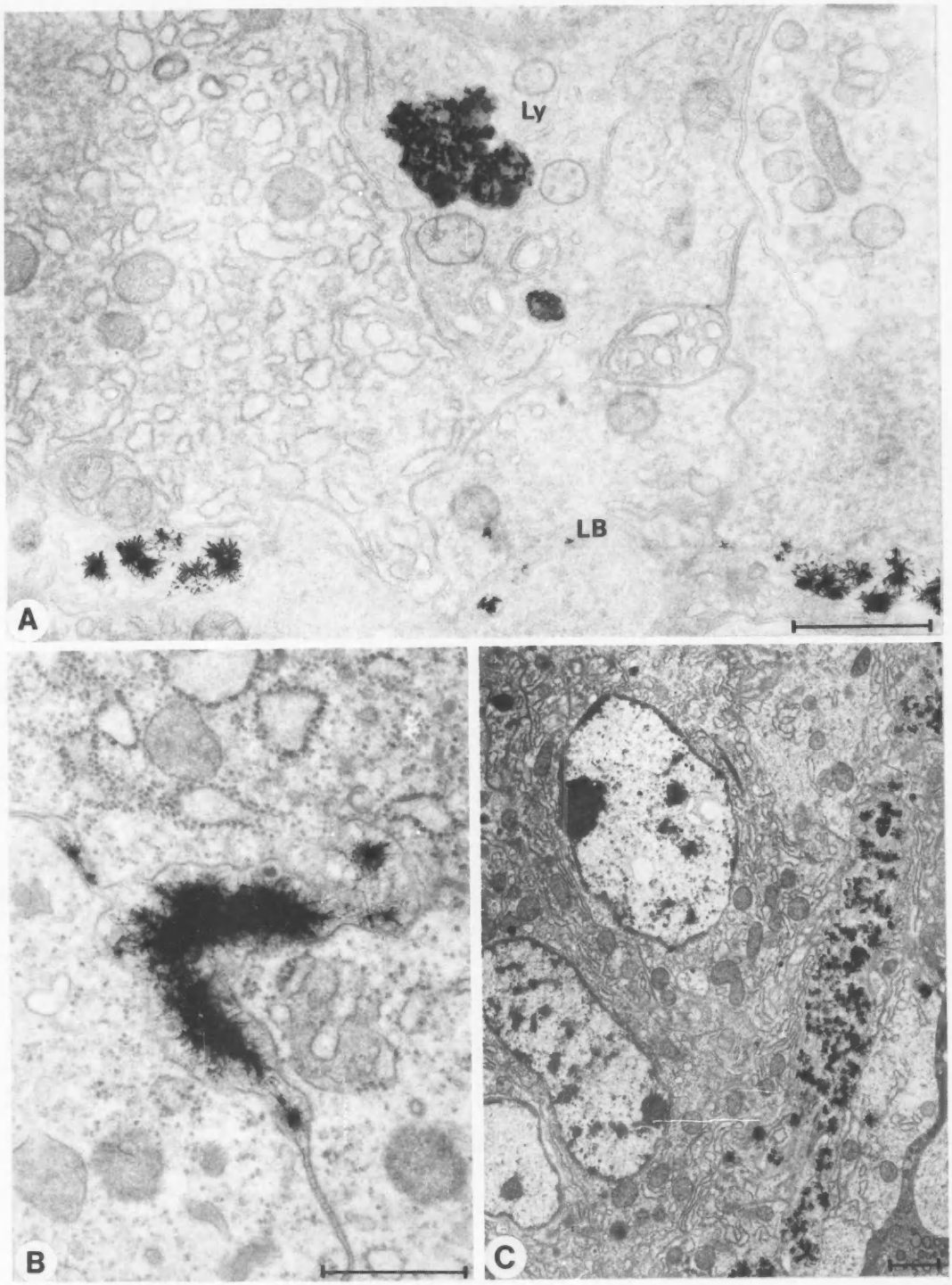

FIG. 5. Huître contaminée par l'Ag dissous dans l'eau. Aspect ultrastructural de la glande digestive. A) Région basale d'une cellule digestive, avec accumulation de sulfure d'argent dans un lysosome (Ly) et dans la lame basale (LB). B) Précipités de sulfure dans un espace entre deux cellules digestives. C) Accumulation de sulfure dans la lame basale. Les échelles représentent respectivement 1, 0,5 et 1 μm.

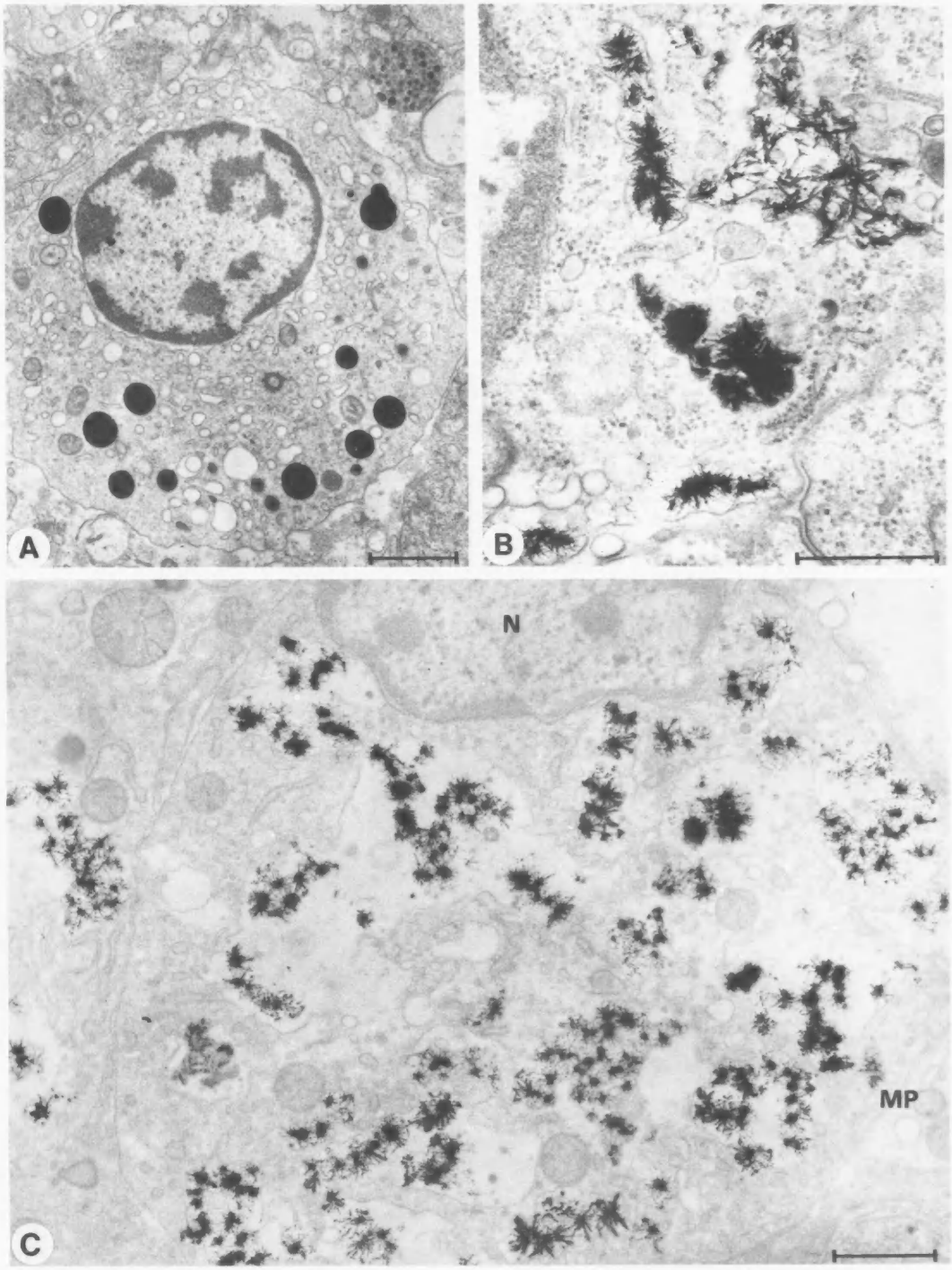

FIG. 6. Aspect ultrastructural des amoebocytes. A) Huître témoin. L'amoebocyte renferme des vacuoles et des inclusions denses. B) Précipités de sulfure d'argent dans le système vacuolaire d'une huître contaminée. C) Coupe non contrastée d'un amoebocyte d'huître contaminée, montrant l'opacité naturelle des précipités de sulfure et l'importance du dépôt d'Ag. Les échelles représentent respectivement 1, 0,5 et 1 μm. MP : membrane plasmique ; N : noyau.

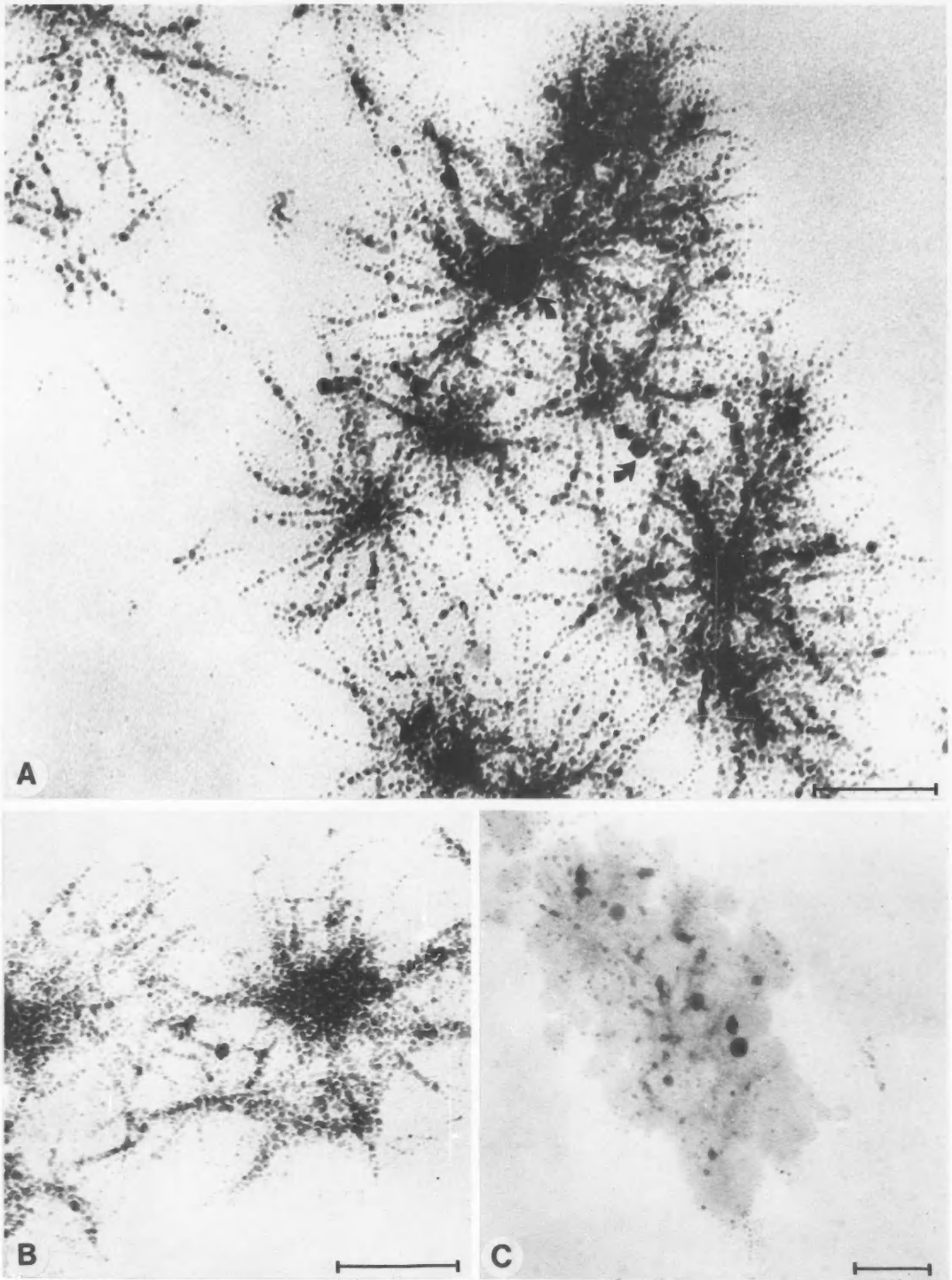

FIG. 7. Aspect ultrastructural des dépôts d'Ag. A) Fixation au glutaraldéhyde. Remarquer la forte opacité des microgranules et la présence de sphères (flèches). B) Fixation au Carnoy. L'opacité des microgranules est plus faible et les sphères manquent. C) Traitement par le ferricyanure ferrique d'une coupe de pièce fixée au glutaraldéhyde. Remarquer la désorganisation des précipités et l'apparition d'un halo dense qui correspond à un mélange de bleu de Prusse, de ferrocyanure d'argent et éventuellement de chlorure d'argent. L'échelle représente, pour les trois clichés, 0,1 μm.

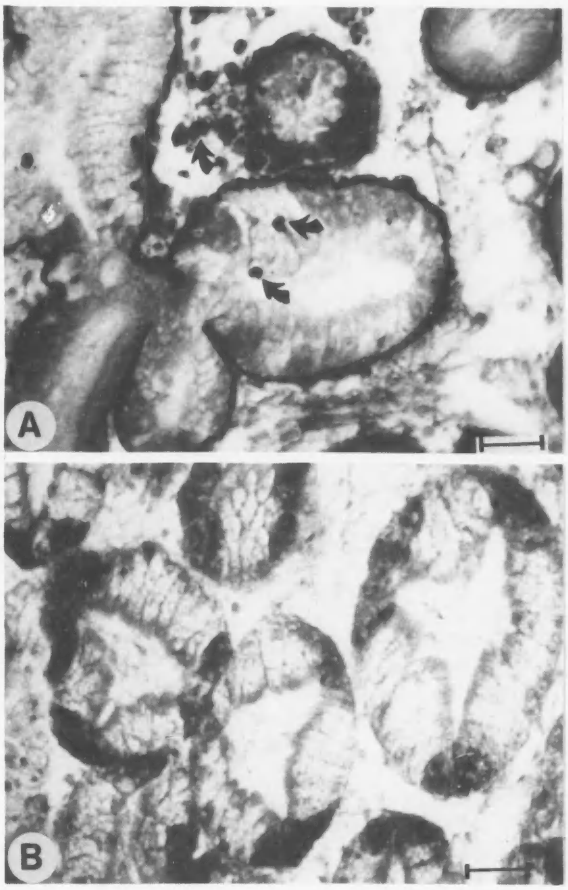

FIG. 8. Réaction de réduction du ferricyanure ferrique sur des coupes de glande digestive d'huître contaminée (A) et d'huître témoin (B). Remarquer, sur la coupe d'huître contaminée, la forte réactivité des lames basales et des amoebocytes (flèches) situés les uns entre les diverticules, les autres dans l'épithélium des diverticules. Coloration de fond par le rouge solide ; l'échelle représente 20 μm.

temps, il est possible d'établir le pourcentage d'Ag accumulé (tableau 1). Après 14 d de contamination, les huîtres ont accumulé une fraction plus importante de l'Ag incorporé dans la nourriture que de l'Ag dissous dans l'eau. L'état d'équilibre entre les organismes et leur milieu étant atteint dès le 14e jour et les apports d'Ag étant constants pendant toute la durée de l'expérience, le pourcentage accumulé par les huîtres n'a plus de signification au-delà du 14e jour.

Si en pourcentage la nourriture représente un vecteur relativement important de transfert, les quantités d'Ag disponibles dans l'eau sont considérablement plus élevées que les apports par voie alimentaire et ceci bien que l'on parte de concentrations identiques dans le milieu de culture des algues et dans le milieu d'élevage des huîtres (schéma 1).

Caractérisation des formes biochimiques de l'Ag dans la fraction soluble des tissus mous

Chez les témoins, le pourcentage d'Ag insoluble présent dans le culot de centrifugation et, après tamisage moléculaire, dans

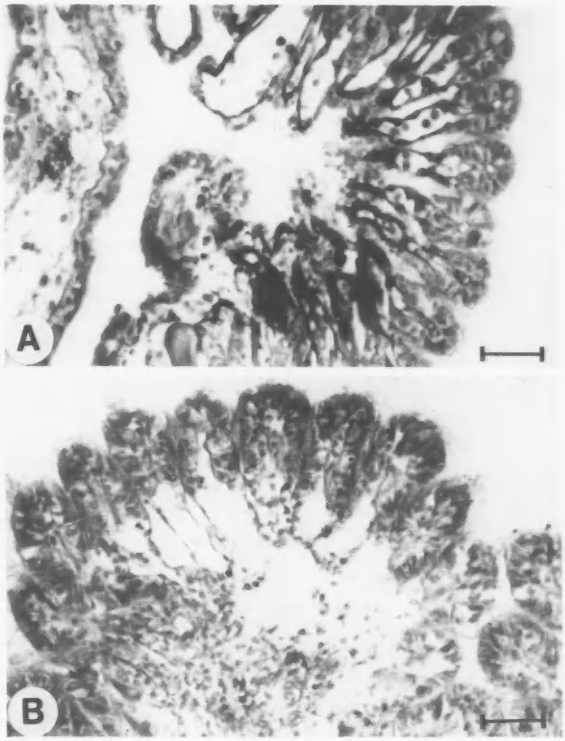

FIG. 9. Réaction de réduction du ferricyanure ferrique sur des coupes de branchie d'huître contaminée (A) et d'huître témoin (B). Remarquer la forte réactivité des lames basales de l'huître contaminée. Coloration de fond au rouge solide ; l'échelle représente 40 μm.

les fractions correspondant au pic d'exclusion, est de 44 %. Il atteint 73 % chez les huîtres contaminées par l'eau. Le passage de l'échantillon sur la colonne de tamisage moléculaire n'induit pas de perte notable d'Ag, puisque 87 % du métal présent avant tamisage se retrouvent dans les différentes fractions éluées (moyenne calculée sur les échantillons d'huîtres polluées ou non). Après contamination, la répartition de l'Ag dans les fractions solubles séparées par tamisage moléculaire présente deux pics α et β (fig. 2) ; selon les individus, le pic α représente 19,5 à 28,4 % de l'Ag soluble, le pic β 32,6 à 38,9 %. Ils correspondent à un pic étalé de la densité optique représentant des composés dont les poids moléculaires apparents (calculés d'après la courbe de calibration de la colonne CL 4B) sont respectivement de 290 000 et de 22 000. Toutefois, lors d'un essai précédent sur Sephadex G75, l'ensemble des molécules liant l'Ag avaient été retrouvées dans le pic d'exclusion, alors qu'un composé de poids moléculaire réel de 22 000 aurait dû être mis en évidence par cette technique. Par ailleurs, lors de la calibration de la colonne Sepharose CL 4B avec des molécules de références seules, le volume total correspondant aux molécules plus petites que celles susceptibles d'être séparées par cette colonne apparaît pour la fraction 64 tandis que lors du tamisage des échantillons d'huître (fig. 2), il apparaît pour la fraction 68. L'ensemble de ces données semble indiquer une rétention sur la colonne de certains composés qui pourraient interférer avec les molécules correspondant aux pics α et β d'Ag. Chez les témoins, les concentrations maximales d'Ag se retrouvent dans les mêmes fractions (38 à 63) mais sans individualisation des

pics α et β caractéristiques des huîtres contaminées (fig. 3). Les courbes de densité optique sont semblables, que les animaux aient été exposés ou non à l'Ag en surcharge et dans tous les cas, le spectre de densité optique des fractions contenant l'Ag présente un maximum pour les longueurs d'onde de 265 à 275 nm avec une dérivée première caractéristique d'une protéine (fig. 4). Le rapport entre les densités optiques à 250 et 280 nm est identique dans les fractions équivalentes des huîtres témoins ou contaminées et il est considérablement plus faible que la valeur caractéristique des métallothionéines de vertébrés. Toutefois, d'après Fowler *et al.* (1986), les protéines fixant les métaux semblent, chez les invertébrés, plus sensibles aux procédures expérimentales que chez les vertébrés. Ainsi, en ce qui concerne le rapport 250/280, ces auteurs ont montré qu'il pouvait varier de 17:1 à 2:1 selon les étapes de mise en évidence de la métalloprotéine.

Des quantités importantes de thiols sont présentes dans la zone d'élution des composés liant l'Ag (fig. 2 et 3). Au niveau des pics α et β, les rapports stoechiométriques moyens (concentration SH/concentration Ag) sont respectivement de 3,3 et 2,5. Toutefois, les concentrations maximales de thiols ne correspondent pas aux concentrations maximales d'Ag et les teneurs en thiols ne sont pas plus élevées chez les huîtres contaminées que chez les témoins (fig. 2 et 3).

Les formes solubles de l'Ag sont donc liées à des composés protéiques dont les caractéristiques sont notablement différentes de celles des métallothionéines de vertébrés.

Accumulation de l'Ag aux niveaux histologique et cytologique

L'Ag forme des précipités dans des inclusions cellulaires ainsi que dans les lames basales de la plupart des tissus. Lorsque le dépôt est important, les lames basales et les cellules les plus riches en précipités acquièrent une teinte brune (fig. 10 A). Le stockage n'étant important que dans les huîtres soumises à la contamination par l'eau ou par les deux voies, les aspects cytologiques et chimiques de l'accumulation du polluant seront d'abord envisagés chez les huîtres soumises à ces protocoles expérimentaux.

Huîtres contaminées par l'eau ou par l'eau et la nourriture

Accumulation intracellulaire de l'Ag — Dans l'épithélium branchial, les cellules absorbantes renferment de petits lysosomes, assez rares, dans lesquels la microanalyse révèle de l'Ag coexistant avec de l'Al, du P, du S, du Fe et du Cu. Les cellules de l'épithélium intestinal contiennent de nombreux lysosomes apicaux qui, chez les témoins, sont des sites d'accumulation de nombreux éléments (Al, P, S, Fe, Ni, Cu) ; après contamination, il s'y ajoute de l'Ag. Dans les cellules digestives des tubules hépato-pancréatiques, les vacuoles qui stockent de nombreux éléments naturels ainsi que des polluants, ne contiennent jamais d'Ag ; seuls de rares lysosomes en renferment (fig. 5 A). Dans les cellules de l'épithélium palléal apparaissent également de volumineux lysosomes contenant le polluant ; le stockage, relativement peu important, est sans relation morphologique avec l'accumulation naturelle de Ca et de Fe qui caractérise cet épithélium. Dans le tissu vésiculeux, les rares cellules à pores qu'il a été possible d'observer émettent également de faibles signaux Ag à la microsonde électronique. Mais de tous les types cellulaires, ce sont les amoebocytes qui assurent le stockage le plus important du polluant (fig. 6) ; leur cytoplasme est rempli de vacuoles claires d'un diamètre de 0,9 à 1,2 µm contenant un abondant précipité d'Ag ; les inclusions

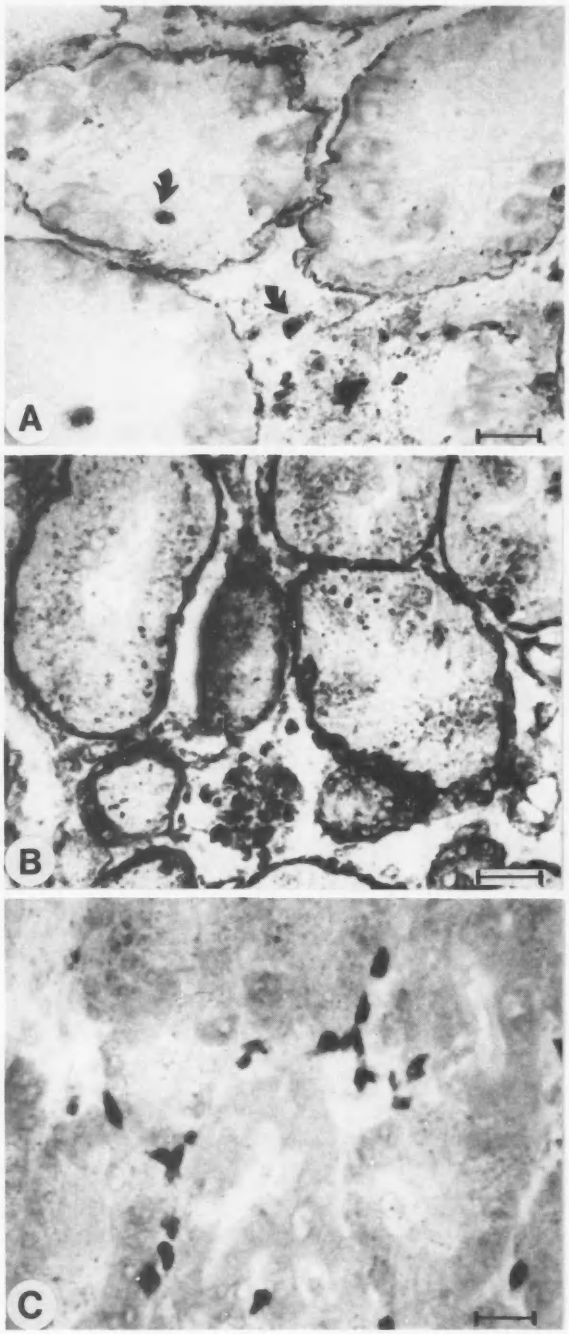

FIG. 10. Diverticules digestifs d'huîtres contaminées (A et B) et d'huître témoin (C). A) Dépôt d'Ag produit par la seule contamination, au niveau des lames basales et des amoebocytes (flèches). Le traitement des coupes par le nitrate d'argent provoque un dépôt supplémentaire d'Ag sur la coupe d'huître contaminée (B), mais non sur celle d'huître témoin (C) ; sur cette dernière, seuls les amoebocytes, en raison de leur richesse en phosphate, réagissent. Coloration de fond au rouge solide ; l'échelle représente 20 µm.

habituelles des amoebocytes, caractérisées par du Zn et du Cu naturels, deviennent rares ou disparaissent. Ces amoebocytes sont particulièrement nombreux dans la glande digestive, les palpes labiaux et le coeur.

Accumulation extracellulaire de l'Ag — Les lames basales de tous les organes sont chargées d'un précipité très opaque aux électrons, identique à celui des vacuoles des amoebocytes. C'est dans la basale des diverticules digestifs, qui est épaissie, que les précipités sont les plus abondants (fig. 5 C) ; parfois, les espaces intercellulaires contiennent également des précipités (fig. 5 B), mais ils ne sont pas rejetés dans la lumière.

Aspect morphologique et analyse élémentaire des précipités — Après fixation au glutaraldéhyde, les précipités comprennent deux types de structure (fig. 7 A). De longues aiguilles de 100 à 200 nm, rayonnant à partir d'un centre, sont constituées d'un alignement de microgranules de forme approximativement cubique et d'un diamètre de 2 à 3 nm. De nombreux amas en forme de sphères, très opaques et d'un diamètre de 10 à 45 nm, sont situés au voisinage des faisceaux de microgranules ou parmi eux. Après fixation au Carnoy, les sphères sont beaucoup moins nombreuses et l'opacité des microgranules est moindre (fig. 7 B). Les sphères sont donc, dans leur majorité, des précipités artéfactuels imputables au glutaraldéhyde.

L'analyse élémentaire de coupes à la paraffine (pièces fixées au Carnoy) ne révèle que deux éléments, S et Ag ; celle de coupes ultrafines (pièces fixées au glutaraldéhyde) indique également la présence de Cu. Il est donc possible que le Cu soit un constituant des sphères.

Composition moléculaire des précipités — Le caractère cytochimique le plus singulier des lames basales et des amoebocytes est leur intense pouvoir de réduction du ferricyanure ferrique, pouvoir que ne possèdent pas les structures et cellules analogues des témoins (fig. 8, 9). Les principaux composés qui, dans les tissus d'invertébrés, manifestent ce pouvoir réducteur sont les protéines sulfhydrilées et certains composés puriques (acide urique, urates). La présence de déchets puriques ne peut être retenue ici en raison de l'insolubilité du composé réducteur dans le carbonate de lithium et l'hydrate de pipérazine (voir Pearse 1972). Des protéines qui assurent la capture de métaux (Cd, Cu) par leurs résidus cystéine ont déjà été caractérisées dans les amoebocytes des huîtres (Martoja et Martin 1985 ; Amiard *et al.* 1986) ; elles sont précisément révélables par le ferricyanure ferrique dont le pH acide libère les métaux et restaure ainsi la réactivité des thiols. Dans le cas des huîtres exposées à l'Ag, des contrôles effectués à la microsonde montrent que la réduction a lieu sans élimination du métal ; dans l'éventualité d'une protéine sulfhydrilée, celle-ci ne complexerait donc pas le métal par ses résidus cystéine. Mais cette hypothèse d'une protéine sulfhydrilée doit également être écartée ; en effet, les propriétés réductrices ne sont pas abolies par un blocage à la *N*-éthylmaléimide, et la réaction au D.D.D. est très faible et identique à celle des témoins. Enfin, l'application de la réaction de Schmorl aux coupes ultrafines montre que ce sont bien les précipités, et non d'autres constituants des basales ou des amoebocytes, qui possèdent les propriétés réductrices (fig. 7 C).

Les précipités (aiguilles et sphères) sont solubles dans l'acide nitrique, le cyanure de potassium et l'acide periodique, alors qu'ils sont intégralement conservés par l'acide sulfurique 1 M. Lorsque le traitement par KCN est effectué sur des coupes à la paraffine, l'analyse à la microsonde montre que la solubilisation concerne à la fois l'Ag et le S ; plus généralement, quelque soit le solvant, il est impossible d'éliminer l'Ag en conservant le S. Toutes ces données confirment que le site fixateur du métal ne peut être ni un groupement thiol, ni un groupe sulfate de mucopolysaccharide, et que la combinaison Ag–S doit être minérale.

Les caractères de solubilité des aiguilles et des sphères, ainsi que leur couleur brunâtre correspondent à la fois à ceux de l'Ag et du sulfure d'argent. Une réduction du ferricyanure ferrique par l'Ag métallique est plausible : c'était un procédé classique de virage en bleu des clichés photographiques. Une réduction par le sulfure d'argent est également envisageable; l'oxydation par le ferricyanure de potassium en milieu alcalin (pH 9) est en

TABLEAU 2. Valeurs de divers rapports théoriques, calculés, ou mesurés par analyse de coupes ultrafines à la microsonde Camebax. La relation $\frac{C\,Ag}{C\,S} = k \cdot \frac{I\,Ag}{I\,S}$, où C = concentration massique et I = intensité mesurée des signaux X, permet à partir du rapport $\frac{I\,Ag}{I\,S}$ obtenu pour le standard d'Ag_2S, de calculer k = 1,86. Il est alors possible de déterminer le rapport massique $\frac{C\,Ag}{C\,S}$ et le rapport atomique $\frac{Ag}{S}$ pour les précipités des lames basales. Les divers rapports déterminés pour les précipités des basales sont comparés à ceux de combinaisons chimiques de composition atomique [1 Ag – 3 S] (caractéristique de métallothionéine), [1 Ag – 1 S] (précipités de *Mytilus*, George *et al.* 1986) et [3 Ag – 1 S]. L'intensité d'émission X a été mesurée en nombre de coups/10 s pour le standard (30 points analysés) et le nombre de coups/100 s pour les lames basales (50 points analysés). L'écart type a été calculé à partir de $\sigma = \sqrt{\frac{\Sigma\,(x_i - x)^2}{n-1}}$.

Composition atomique		1 Ag – 3 S	1 Ag – 1 S	Standard de Ag_2S 2 Ag – 1 S	Huîtres Carnoy	Huîtres Glutaraldéhyde	3 Ag – 1 S
$\frac{I\,Ag}{I\,S}$	Mesuré			3,61 ± 0,03	3,07 ± 0,19	4,45 ± 0,76	
	Calculé	0,6	1,8				5,4
$\frac{C\,Ag}{C\,S}$	Théorique	1,12	3,36	6,73			10,09
	Calculé				5,7	8,3	
k	Calculé			1,86			
$\frac{Ag}{S}$	Théorique	1/3	1	2			
	Calculé				1,7 ± 0,1	2,5 ± 0,5	3

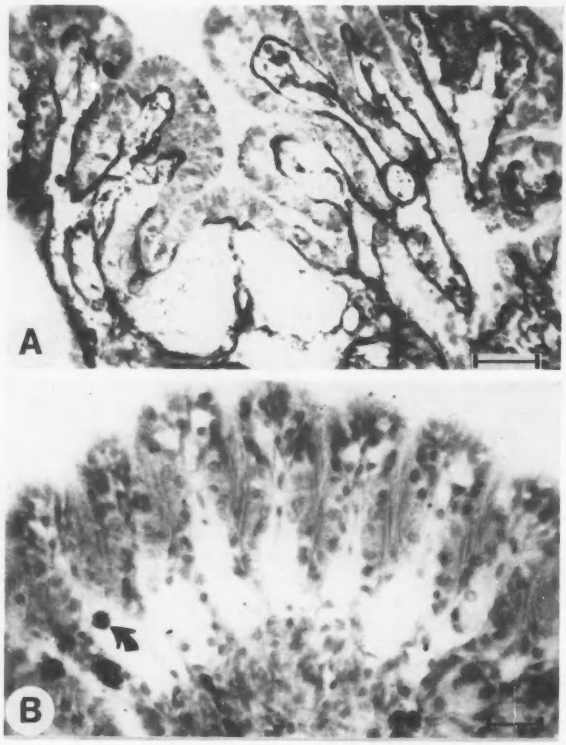

FIG. 11. Traitement par le nitrate d'argent de coupes de branchie d'huître contaminée (A) et d'huître témoin (B). La capture d'Ag est importante sur les lames basales de l'huître contaminée, nulle sur celles de l'huître témoin où seuls les amoebocytes (flèche) présentent leur réactivité naturelle. Coloration de fond au rouge solide ; l'échelle représente 40 µm.

effet une méthode de dosage des sulfures solubles (Charlot 1974) :

$$2\ Fe(CN)_6^{3-} + S^{2-} \longrightarrow 2\ Fe(CN)_6^{4-} + S.$$

L'oxydation d'un sulfure très peu soluble tel que Ag_2S est évidemment plus difficile. Plus précisément, il n'est possible $E^\circ_{S/S^{2-}}$ de dissoudre une quantité donnée de Ag_2S par la réaction $Ag_2S \longrightarrow 2\ Ag^+ + S + 2e^-$, qu'à la condition que le potentiel de la solution soit supérieur à la valeur :

$$E_{min} = E^\circ_{S/S^{2-}} - 0{,}0295 \log K_S + 0{,}059 \log (Ag^+)$$

où $E^\circ_{S/S^{2-}}$ est le potentiel standard du couple S/S^{2-}, K_S le produit de solubilité du sulfure d'argent et (Ag^+) l'activité des ions Ag^+ qui sera assimilée à leur concentration, $E^\circ_{S/S^{2-}} = -0{,}48\ V$/E.N.H. et $K_S = 1{,}6 \times 10^{-49}$ à 18°C.

Une coupe histologique de 7 µm d'épaisseur contient, d'après les dosages d'huîtres, au maximum 0,02 µg d'Ag inorganique, et elle est traitée par 25 mL de réactif. Si l'on suppose que cet Ag est pour l'essentiel sous forme de sulfure, la concentration en Ag^+ après réaction est au maximum de $6{,}4 \times 10^{-9}$ mol·L^{-1}.

On en déduit $E_{min} \leqslant 0{,}46\ V$. Or la mesure du potentiel du réactif a donné une valeur de l'ordre de 1,1 *V*. Dans ces conditions, l'oxydation de Ag_2S est thermodynamiquement possible. Elle est même plus favorisée que ne l'indiquent les calculs précédents si les ions Ag^+ reprécipitent sous une forme différente de Ag_2S, ce qui a pour effet d'abaisser leur activité; or tel doit être le cas puisque l'analyse à la microsonde montre que le traitement n'élimine pas l'Ag de manière significative. Certes, il est très possible que la transformation de Ag_2S ne soit que partielle, mais on peut aussi envisager que Ag^+ libéré se retrouve sous forme de AgCl, de $Ag_4[Fe(CN)_6]$ et de $AgFe^{II}Fe^{III}(CN)_6$: le réactif contient en effet des ions Cl^- et le produit de solubilité peut être atteint — dans l'hypothèse d'une transformation complète de Ag_2S — pour les structures les plus riches en Ag; par ailleurs, les ferrocyanures des métaux lourds sont connus pour être peu solubles. Le traitement, par le ferricyanure ferrique, de coupes histologiques contenant un mélange de sulfure d'argent et d'Ag métallique peut donc donner lieu aux réactions suivantes :

a) réduction par le sulfure d'argent :

$$12\ K_3[Fe(CN)_6] + 4\ FeCl_3 + 6\ Ag_2S \longrightarrow Fe_4[Fe(CN)_6]_3 + 9\ K_4[Fe(CN)_6] + 12\ AgCl + 6S$$

et/ou :

$$4\ K_3[Fe(CN)_6] + 4\ FeCl_3 + 2\ Ag_2S \longrightarrow Fe_4[Fe(CN)_6]_3 + Ag_4[Fe(CN)_6] + 12\ KCl + 2S$$

b) réduction par l'Ag métallique (Dubusc *et al.* 1979) :

$$12\ K_3[Fe(CN)_6] + 4\ FeCl_3 + 12\ Ag \longrightarrow Fe_4[Fe(CN)_6]_3 + 9\ K_4[Fe(CN)_6] + 12\ AgCl$$

et/ou :

$$4\ K_3[Fe(CN)_6] + 4\ FeCl_3 + 4\ Ag \longrightarrow Fe_4[Fe(CN)_6]_3 + Ag_4[Fe(CN)_6] + 12\ KCl.$$

En conséquence, si l'on considère les caractères de solubilité, le pouvoir réducteur et une forte relation entre le S et l'Ag, les précipités pourraient être formés de sulfure d'argent, ou d'un mélange de sulfure d'argent et d'Ag métallique.

Un calcul du rapport atomique Ag/S a été effectué par analyse de coupes ultrafines de lames basales fixées au Carnoy et au glutaraldéhyde et d'une coupe analogue d'un témoin mince (échantillon de Ag_2S, pureté 99,9 %). Ce rapport, qui est de 2 pour le standard, est de 1,7 ± 0,1 pour les précipités fixés au Carnoy et de 2,5 ± 0,5 pour ceux fixés au glutaraldéhyde (tableau 2). Lorsque les sphères sont peu nombreuses (fixation au Carnoy), le rapport est donc très voisin de celui du sulfure d'argent ; la faible différence peut être attribuée au S organique naturel (ponts disulfures) des protéines des lames basales. De plus, la valeur de 1,7 est beaucoup trop élevée pour que, comme chez *Mytilus* (George *et al.* 1986), elle puisse correspondre à une liaison entre un atome d'Ag et un groupe sulfate ou thiol. Par ailleurs, les valeurs sont, pour les basales fixées au glutaraldéhyde, à la fois très dispersées et supérieures à celles du standard ; l'abondance de sphères se traduit donc par un excès d'Ag pouvant atteindre jusqu'à 30 %.

Connaissant le fort pouvoir réducteur des aldéhydes à l'égard des complexes argentiques, on est conduit à l'interprétation suivante. Il existe, *in vivo*, des microgranules de sulfure d'argent et de rares sphères dont la nature chimique n'a pu être déterminée. La fixation par le glutaraldéhyde provoque la précipitation d'Ag métallique aux dépens de complexes organiques de l'Ag ; le métal précipité formerait de nouvelles sphères et se déposerait à la surface des microgranules de sulfure, augmentant ainsi leur opacité aux électrons. La présence de ligands autres que S^{2-} est confirmée par l'aptitude des lames basales à

fixer, *in vivo*, de l'Ag excédentaire : lorsque des coupes à la paraffine d'huîtres contaminées sont traitées par le nitrate d'argent, un important dépôt d'Ag s'ajoute au sulfure préexistant, alors que la capture du métal est nulle chez les témoins (fig. 10, 11). À l'échelle ultrastructurale, cette même réaction provoque l'apparition de sphères surnuméraires.

En conclusion, il existe dans les lames basales des huîtres contaminées du sulfure d'argent accompagné de ligands organiques capables de complexer l'Ag et incomplètement saturés. Dans les inclusions des amoebocytes, la présence de sphères est également signalétique de ligands organiques ; mais en raison des caractères particuliers de ces cellules (forte réactivité naturelle à la méthode de von Kossa imputable à des sels minéraux), il est impossible de déterminer si ces ligands sont saturés. Quoi qu'il en soit, ces ligands doivent correspondre aux protéines de complexation isolées par les techniques biochimiques.

Huîtres contaminées par la nourriture seule

Quel que soit l'organe, la contamination ne provoque aucune accumulation intracellulaire d'Ag. Les amoebocytes, en particulier, bien que très nombreux, ne réduisent pas le ferricyanure ferrique. Seules les lames basales des diverticules digestifs contiennent les précipités caractéristiques ; mais ils sont moins nombreux que dans les huîtres contaminées par l'eau ou par les deux voies, et leur distribution n'est pas uniforme. Il en résulte que seuls certains segments des lames basales réagissent positivement à la réaction de Schmorl. Cependant, les basales dans leur ensemble manifestent une forte capacité de complexation, *in vitro*, de l'Ag excédentaire, démontrant ainsi la présence des protéines de capture du métal.

Discussion

Une contamination identique de l'eau d'élevage et du milieu où sont cultivées les algues utilisées comme nourriture, permet d'évaluer l'importance relative des voies de transfert menant à une contamination des tissus de l'Huître. La contamination par l'eau induit des concentrations d'Ag plus fortes que le transfert du polluant par voie alimentaire. Toutefois, cette dernière n'est pas négligeable puisqu'un pourcentage relativement élevé du métal incorporé dans le phytoplancton est assimilé par l'huître.

Quel que soit le mode d'exposition, la concentration en Ag des huîtres atteint une valeur maximale au plus tard le 14^{e} jour. Ce plateau correspond vraisemblablement à la mise en place, après un temps de latence inférieur à 2 sem, d'un système d'élimination du métal qui stabilise les niveaux de concentration, différents d'ailleurs selon les modes d'exposition. De la même façon, il s'établit rapidement, chez la Scrobiculaire, un équilibre entre le milieu interne du mollusque et son environnement (Amiard 1978a).

L'Ag forme, dans l'organisme de l'huître, des combinaisons organiques et une combinaison minérale. Seules les premières avaient déjà été étudiées chez les Bivalves. Elles comprennent des protéines de poids moléculaire élevé et des protéines apparentées aux métallothionéines (metallothionein-like proteins), quantitativement moins importantes que les précédentes. Chez *Macoma balthica* exposée à l'Ag dans un site pollué, le métal est surtout lié à des protéines de poids moléculaire supérieur à 100 000 et moins de 10 % est complexé par une « metallothionein-like protein » (Bray *et al.* 1983). Pour *Mytilus edulis*, le pourcentage d'Ag de la fraction soluble (45 à 55 %) est beaucoup plus élevé que celui que nous avons déterminé chez *Crassostrea* ; 92 % de l'Ag de cette fraction est, chez les juvéniles, lié à des molécules de poids moléculaire très élevé, alors que chez les adultes, ce pourcentage n'est que de 77 %. Chez ces derniers seulement, 20 % de l'Ag soluble est élué dans une fraction dont la composition en acides aminés est très semblable à celle de Cu- or Hg-thionéines (George *et al.* 1986). De telles protéines peuvent être induites chez les huîtres par différents métaux des groupes IB et IIB. Divers auteurs considèrent en effet que le Cu et le Cd seraient complexés par une « metallothionein-like protein » (Casterline et Yip 1975 ; Frazier 1979 ; Sharma 1983). De même, la glande digestive d'échantillons récoltés *in situ* contient une protéine qui possède plusieurs caractères des métallothionéines (Thompson et Cosson 1984). Enfin, les huîtres contaminées expérimentalement par le Cd produisent une protéine qui correspondrait à deux isométallothionéines de pH 6,2 et 5,95 (Gillot 1987). Toutefois, l'interprétation des résultats concernant les protéines de faible poids moléculaire liant les métaux chez les huîtres est très délicate (Fowler *et al.* 1986 ; Imber *et al.* 1987) et aucun auteur ne peut se prononcer de façon définitive sur la nature exacte de ces protéines. Dans la présente étude, la fraction soluble de l'Ag est liée à des complexes protéiques dont les caractéristiques diffèrent notablement de celles des « metallothionein-like proteins. » Pour expliquer nos résultats, deux interprétations sont possibles : ou bien contrairement au Cu et au Cd, l'Ag n'induit pas, chez l'Huître, la synthèse de protéines apparentées à la métallothionéine, ou bien comme chez la Moule (George *et al.* 1986), l'induction n'est pas encore possible chez les jeunes individus où seules interviennent les protéines qui fixent le métal naturel.

La combinaison minérale est du sulfure d'argent qui assure la bioaccumulation de plus de 70 % du métal chez les huîtres contaminées. La précipitation du sulfure peut être considérée comme la dernière étape du catabolisme d'Ag-protéines, interprétation précédemment proposée pour les espèces de mollusques qui accumulent de façon naturelle l'Ag et le Cu (Martoja *et al.* 1985). Ce mécanisme n'est pas non plus sans rappeler la précipitation de séléniure de mercure aux dépens de sélénoprotéines de complexation de Hg qui a lieu chez les Mammifères (Martoja et Berry 1980). La formation de combinaisons minérales entre métaux des groupes IB–IIB et éléments du groupe VIA paraît donc assez fréquente chez les animaux. Pour les Mollusques cependant, selon que les métaux accumulés ont une origine naturelle ou qu'ils proviennent de contamination, il peut exister des différences à la fois dans les formes chimiques de stockage et dans les structures histologiques qui les réalisent. Ainsi, le Cu naturel est précipité en sulfure dans les cellules à pores, alors qu'après contamination, il est accumulé dans les amoebocytes sous forme d'un complexe protéique, ainsi que dans la glande digestive et dans les branchies (Amiard *et al.* 1986). Pour l'Ag, du sulfure précipite aussi bien dans les conditions naturelles qu'après contamination ; mais les structures histologiques impliquées diffèrent : cellules à pores dans les conditions naturelles (Martoja *et al.* 1985), cellules à pores et surtout amoebocytes et lames basales après contamination. La localisation extra-cellulaire de l'Ag est une particularité du métal, indépendante de l'espèce animale, puisqu'elle est connue à la fois chez d'autres Mollusques et chez les Mammifères. Cette analogie n'est pas seulement histologique, mais aussi chimique ; les dépôts d'Ag caractéristiques de l'argyrose des mammifères seraient en effet constitués de sulfure d'argent (Dempsey 1973 ; Dempsey *et al.* 1973) provenant du catabolisme d'une Ag-protéine (Venugopal et Luckey 1974). La production du ligand S^{2-} doit avoir pour origine une désulfhydra-

tion des acides aminés soufrés, en particulier ceux des protéines de complexation du métal que nous avons isolées. L'existence de cette voie catabolique dans les vacuoles des amoebocytes n'est pas surprenante, si l'on assimile ces vacuoles à des lysosomes. En revanche, la formation de sulfure dans les lames basales, qu'il s'agisse des Mammifères ou de l'Huître, est difficile à interpréter. Plusieurs arguments sont en faveur d'une précipitation *in situ* du sel minéral. En premier lieu, des protéines de complexation d'Ag, que nous considérons comme des précurseurs du sulfure, sont présentes dans les basales. En second lieu, l'arrangement des granules en files régulières rayonnant à partir d'un centre indique leur addition successive à partir d'un point de nucléation. Enfin, aucun granule de sulfure et *a fortiori* aucune image d'extrusion n'a été observée dans le hyaloplasme des cellules bordant les lames basales. L'origine des enzymes impliquées dans ce catabolisme reste évidemment à déterminer.

Nos résultats permettent de concevoir les relations entre un mollusque et les diverses sources d'Ag exogène, de retracer le cycle du métal dans l'organisme et de prévoir, d'un point de vue écotoxicologique, les conséquences de contamination des milieux naturels. Les formes solubles sont fortement assimilables ; ce sont les chloroargentates $AgCl_4^{3-}$, $AgCl_3^{2-}$ et $AgCl_2^-$ (Bowen 1985). Le métal incorporé par le phytoplancton est également bien assimilé ; les algues réalisent donc des combinaisons chimiques biodégradables dont la nature n'est pas encore connue. Enfin, dans un milieu naturel, il conviendrait de considérer l'Ag adsorbé sur des particules d'argile, d'oxydes et d'hydroxydes (Bowen 1985) dont l'importance dans l'alimentation des suspensivores est bien connue. Le métal transite par les épithéliums des branchies, de l'intestin et des diverticules digestifs sans y subir de rétention importante ; ces épithéliums ne constituent donc pas de barrières de diffusion aussi efficaces que pour d'autres métaux (Cu, Cd, Pb) (Jeantet *et al.* 1985 ; Viarengo *et al.* 1985 ; Amiard *et al.* 1986). En raison de son affinité, aux pH physiologiques, pour des acides aminés comme l'arginine, la lysine et l'histidine, l'Ag doit être capté par diverses protéines, en particulier des protéines hémolymphatiques qui en effectuent le transport. À l'inverse de la moule, l'endocytose d'Ag-protéines hémolymphatiques par les cellules à pores est négligeable, la voie d'épuration conduisant surtout à la précipitation de sulfure dans les amoebocytes et dans les lames basales. La concentration importante du métal dans la glande digestive (Amiard 1978b, c) doit ainsi être rapportée non aux processus de digestion, mais au grand développement des lames basales et à l'importance numérique des amoebocytes de ce complexe histologique. Il en est de même pour le coeur, riche en amoebocytes. La très grande stabilité chimique du sulfure permet d'écarter l'éventualité d'une excrétion par dissolution. Pour les lames basales, nous ignorons la destinée du sel minéral lors du renouvellement des molécules de ces structures. Mais pour les amoebocytes, on sait qu'ils sont éliminés après migration au travers de l'épithélium du rein (voir Cheng 1981). Ce mode d'extrusion explique l'existence d'un pallier de concentration traduisant un équilibre entre le flux d'entrée de l'Ag et l'élimination du sulfure par les amoebocytes.

La précipitation de sulfure d'argent constitue un processus de détoxication dont l'efficacité est démontrée par l'absence de lésions cytologiques. Le déroulement normal de la spermatogenèse indique également qu'il n'existe pas d'interactions Ag–ADN susceptibles de perturber les divisions cellulaires (Venugopal et Luckey 1974). Les seuls effets imputables à la contamination sont d'ordre métabolique. L'Ag est en effet connu comme inhibiteur ou réactiveur d'enzymes et ce sont sans doute ces propriétés qui causent les déficiences de stockage du glycogène chez les huîtres contaminées. Ces effets métaboliques, auxquels il convient sans doute d'ajouter une augmentation possible de l'activité respiratoire (Calabrese *et al.* 1977) sont toutefois insuffisants pour altérer les grandes fonctions de l'organisme.

Du point de vue écotoxicologique, on peut prévoir qu'en cas de contamination chronique de l'environnement, la survie de l'espèce serait menacée non par une diminution de la capacité de reproduction des adultes, mais par l'élimination des larves. Celles-ci sont en effet beaucoup plus sensibles aux effets toxiques du métal puisque la concentration létale y est 500 fois plus faible (Calabrese *et al.* 1977). Nos résultats expliquent cette différence entre larves et adultes, puisque la détoxication implique la présence de structures histologiques qui ne se mettent en place que progressivement au cours de la vie larvaire. Quant au transfert de l'Ag dans les réseaux trophiques, il apparaît que le métal incorporé dans le phytoplancton est, au moins en partie, sous une forme chimique utilisable par les consommateurs ; mais l'espèce chimique a pu être modifiée par le traitement de congélation–décongélation subi par les algues. L'huître présente une très grande capacité d'accumulation à l'égard de l'Ag, mais le transfert aux niveaux trophiques plus élevés doit être limité, puisqu'une fraction importante du métal est immobilisée sous une forme physicochimique très stable.

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NOTES

Predicting Nighttime Dissolved Oxygen Loss in Aquaculture Ponds[1]

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The Whole Pond Respiration–Diffusion (WPRD) model was evaluated for brackish-water ponds. The WPRD model accurately describes the nighttime decline of dissolved oxygen concentration (DO) in both freshwater and brackish-water ponds. DO, water temperature, and wind speed were monitored overnight in marine shrimp (*Penaeus vannamei* and *P. monodon*) ponds at Amorient Aquafarm Inc. (Kahuku, Oahu) and at the Mariculture Research and Training Center (Hakipuu, Oahu) during July through December 1986. The model performed well for calm nights (wind speed between 1 and 2 $m \cdot s^{-1}$) and for relatively windy nights (wind speed greater than 7 $m \cdot s^{-1}$). Diffusion of oxygen into the ponds, particularly at Amorient, was important in determining the nighttime DO decline. The model has yielded accurate predictions of dawn DO for a variety of aquaculture ponds and meteorological conditions.

Le modèle de respiration–diffusion dans un étang a été évalué pour des étangs d'eau saumâtre. Ce modèle décrit avec précision la baisse nocturne de la concentration d'oxygène dissous dans les étangs d'eau douce et d'eau saumâtre. L'oxygène dissous, la température de l'eau et la vitesse du vent ont été surveillés pendant la nuit dans les étangs à crevette marine (*Penaeus vannamei* et *P. monodon*) à l'*Amorient Aquafarm Inc.* (Kahuku, Oahu) et au *Mariculture Research and Training Center* (Hakipuu, Oahu) de juillet à décembre 1986. Le modèle s'est bien comporté pendant les nuits calmes (vitesse du vent comprise entre 1 et 2 $m \cdot s^{-1}$) et les nuits relativement venteuses (vitesse du vent supérieure à 7 $m \cdot s^{-1}$). La diffusion de l'oxygène dans les étangs, notamment à Amorient, était un élément important pour calculer la baisse d'oxygène dissous pendant la nuit. Le modèle a permis de formuler des prévisions précises concernant la concentration d'oxygène dissous à l'aube pour divers étangs d'aquaculture et de conditions météorologiques.

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The ability to forecast the dissolved oxygen concentration (DO) at dawn in aquaculture ponds could serve as a valuable management tool. Previous models developed by Boyd et al. (1978) and Romaire (1979) for channel catfish (*Ictalurus punctatus*) ponds in Alabama are inappropriate for systems in which plankton respiration is not the major DO sink or in which nighttime DO decreases are curvilinear (Madenjian et al. 1987a). The pond sediment is frequently the chief consumer of oxygen in freshwater prawn (*Macrobrachium rosenbergii*) ponds in Hawaii. In addition, windy conditions can lead to nonlinear rates of nighttime oxygen decline. Madenjian et al. (1987b) proposed that the Whole Pond Respiration–Diffusion (WPRD) model was appropriate in these Hawaiian systems. In this paper we test the WPRD model for use in marine shrimp (*Penaeus vannamei* and *P. monodon*) ponds.

To apply the WPRD model to brackish-water ponds, the transfer rate of oxygen between seawater and the atmosphere must be accounted for. Downing and Truesdale (1955) found no difference in the rates of oxygen transfer at the air-water interface between salt water and freshwater. In their study, jets of air were forced over the surface of water in laboratory tanks. Similarly, employing a wind tunnel, Merlivat and Mémery (1983) found no difference in rates of gas transfer across the water surface between freshwater and seawater. In contrast, transfer of oxygen across the air–water surface proceeded faster in salt water rather than in freshwater when the water was subjected to the bubbling action of an artificial aerator (G. L. Rogers, unpubl. rep.; M. Zapka and H. Krock, Ocean Engineering Department, University of Hawaii, Honolulu, HI, pers. comm.). Smaller bubble size in seawater than in freshwater may have resulted in a higher rate of oxygen transfer in salt water. Several researchers (Liss 1973; Deacon 1977; Hsu et al. 1984) have reported an increase in bubble density in tanks exposed to winds of increasing velocity in a wind tunnel. However, since the intensity of bubbling from an artificial aerator is conspicuously greater than that from wind reaeration, we assumed equal rates of oxygen transfer by wind reaeration across both freshwater and saltwater pond surfaces for our modeling purposes.

Sampling Methods

From July through August 1986, six overnight monitoring trips were undertaken at Amorient Aquafarm Inc. in Kahuku, Oahu. During each trip, DO and water temperature were meas-

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ured at dusk, approximately 3 h after the dusk sampling, and within 1 h of sunrise. Temperature and DO were measured at pond surface (approximately 10 cm below surface) and bottom (within 10 cm above bottom) at each site using a YSI (Yellow Springs Instrument Co. model 54) dissolved oxygen meter with a field probe and stirrer. DO was sampled at two sites in the pond: one site on the west side and the other on the east side of the pond. Five 0.4-ha ponds (ponds 113, 114, 121, 122, and 123) were monitored during each trip. A total of 30 trials were performed at Amorient.

Overnight wind speed data coinciding with the sampling trips at Amorient were furnished by the Hawaii Natural Energy Institute. Wind speed was monitored from a 24.4-m-high tower within 2 km of the Amorient ponds. An average wind speed for each sampling night was calculated. The average wind speed was adjusted for a height of 10 m above the pond surface using the relationship cited by Madenjian et al. (1987b). Based on sampling two transects in the Amorient ponds, average pond depth was determined; pond depth averaged 0.75 m for the ponds. Amorient ponds were well mixed by wind during the study period and never showed an absolute difference greater than 0.5 mg $O_2 \cdot L^{-1}$ between surface and bottom observed DO values.

The model was also tested at the Mariculture Research and Training Center (MRTC) in Hakipuu, Oahu, using data from an automated data logging system. DO and water temperature were monitored at middepth in four 0.2-ha ponds; in each pond, DO and water temperature were measured every 10 min for an entire grow-out period (August through December 1986). Additionally, wind speed was recorded every 10 s and then averaged every 2.5 min. Water was pumped from one fixed location in each pond (5–10 m from bank of pond) into a sampling chamber located inside a shelter at the center of the four-pond complex. DO and water temperature were measured in the sampling chamber using a Leeds and Northrup field DO probe with model 7932 DO meter and a YSI model 403 temperature probe, respectively. All observations were recorded on computer (Apple IIe) diskette. Predictions of dawn DO were based on a measurement of dusk DO, a second measurement 3 h after the dusk sampling, and the average wind speed for the night. Wind speed at MRTC was measured at 3.9 m above the water surface and was then adjusted for an elevation of 10 m above water level. Average depths of the four ponds at MRTC were estimated using the bathymetric procedures presented by Hutchinson (1957). Pond depths at MRTC were monitored, with average pond depths ranging from 0.6 to 0.9 m during the study. Maximum pond depth did not exceed 1.2 m in any of the ponds. Salinity was measured manually, three times a week, using a refractometer (Atago Tanaka model S-100), which was calibrated with a salinometer (YSI model 33 salinity–conductivity–temperature meter). Salinites observed at the Amorient shrimp ponds ranged from 19 to 34 $g \cdot kg^{-1}$; MRTC pond salinities ranged from 11 to 28 $g \cdot kg^{-1}$. Ponds at MRTC were mixed during the daylight hours by a 0.25-hp pond circulator (Fast et al. 1983) to prevent stratification. A total of 30 trials were analyzed at MRTC.

The Model

The WPRD model described by Madenjian et al. (1987b) was applied to the Amorient and MRTC data with one modification: the oxygen saturation level was adjusted for salinity, as reported by the American Public Health Association et al. (1986). Thus, our model was

TABLE 1. Minimum (min.), maximum (max.), and mean (standard error) of the absolute value of the residuals from fitting the WPRD model to data from marine shrimp ponds at Amorient (Kahuku, Oahu), July through August 1986, and at MRTC (Hakipuu, Oahu), August through December 1986. The dawn DO prediction of the model was based on an observation of DO at dusk and another DO observation approximately 3 h after dusk. The residual is the observed dawn DO minus the predicted dawn DO. At Amorient, DO at the east and west stations were averaged. N = number of trials.

Site	N	Absolute value of residual (mg $O_2 \cdot L^{-1}$)		
		Min.	Max.	Mean (SE)
Amorient	30	0.02	1.00	0.27 (0.04)
MRTC	30	0.05	1.34	0.52 (0.07)
Amorient and MRTC pooled	60	0.02	1.34	0.39 (0.04)

$$(1)\quad \frac{d\,(\mathrm{DO})}{dt} = -ce^{kT} + \frac{\mathrm{KL}}{\mathrm{PD}}\,(\mathrm{SAT}(T,S) - \mathrm{DO})$$

where DO = pond DO (milligrams O_2 per litre), $d(\mathrm{DO})/dt$ = rate of change in pond DO with time (milligrams O_2 per litre per hour), c = respiration coefficient (milligrams O_2 per litre per hour), k = instantaneous rate of increase of respiration with water temperature (per degree Celsius), T = water temperature (degree Celsius), KL = oxygen transfer coefficient (metres per hour), PD = average pond depth (metres), S = salinity (grams per kilogram), and $\mathrm{SAT}(T,S)$ = oxygen saturation level (milligrams O_2 per litre) at water temperature, T (degrees Celsius), and salinity, S (grams per kilogram). Temperature was modeled as decaying exponentially during the night; k was set equal to 0.0542 (Madenjian et al. 1987b).

Model Verification

For the Amorient data, model predictions were based on average pond DO. For both the east and west stations on each pond, surface and bottom observations of DO were averaged. Then, the averages of the west and east stations were averaged to yield the average pond DO. For MRTC data, DO was observed at only one location in the pond. For both the Amorient and MRTC sites, the respiration coefficient, c, was estimated using a numerical analysis technique, such that the prediction curve was fitted through the second DO observation (the DO measurement made approximately 3 h after the dusk DO was observed) (see Madenjian et al. 1987b). A Runge–Kutta numerical integration routine was used to evaluate the integral of the differential equation (equation 1). In addition to the forecasts of dawn DO in the ponds, hourly predictions were generated for the nighttime period and the predicted DO curve for overnight decline was compared with the observed DO curve.

Descriptive statistics were calculated for the absolute value of the residuals (observed DO minus predicted DO) from the WPRD model for both sites (MRTC and Amorient) pooled, as well as both sites separately. Additionally, the predictions of dawn DO from the WPRD model were regressed upon the observed dawn DO values to see how close the slope of such a line was to unity and how close the intercept was to zero.

The net effect of diffusion on the nighttime DO decline observed in the shrimp ponds was estimated in the following manner. The full model (as given in equation 1) was forced through the observed dawn DO and the respiration coefficient

TABLE 2. Observed and predicted dissolved oxygen concentration (DO) at dawn for Amorient marine shrimp ponds (Kahuku, Oahu), July through August 1986. Predictions were based on the WPRD model using a DO measurement at dusk and a second DO measurement approximately 3 h after dusk. DO measurement used was a pond average (DO averaged for observations at east and west sides of pond). The diffusion effect (DE, mg $O_2 \cdot L^{-1}$) was the overnight loss (denoted with a negative sign) or gain of DO due to diffusion. The respiration effect (RE, mg $O_2 \cdot L^{-1}$) was the overnight DO loss due to respiration. Date was for start of sampling period.

Date (mo-d-yr)	Pond	Wind speed ($m \cdot s^{-1}$)	Measured DO (mg $O_2 \cdot L^{-1}$)			Predicted dawn DO	Residual	DE	RE
			Dusk	3 h after dusk	Dawn				
07-26-86	113	10.07	9.80	6.99	4.60	4.65	−0.05	0.95	6.15
07-26-86	114	10.07	6.11	5.34	4.53	4.82	−0.29	2.86	4.45
07-26-86	121	10.07	5.14	4.21	3.29	3.56	−0.26	4.12	5.96
07-26-86	122	10.07	8.83	7.10	5.09	5.57	−0.48	0.41	4.15
07-26-86	123	10.07	10.06	7.72	5.24	5.61	−0.37	−0.46	4.36
08-02-86	113	8.00	5.96	4.19	2.75	2.52	0.23	2.86	6.07
08-02-86	114	8.00	6.99	5.71	4.18	4.44	−0.26	1.55	4.36
08-02-86	121	8.00	7.84	6.38	4.36	4.77	−0.41	0.87	4.35
08-02-86	122	8.00	8.26	6.78	5.19	5.09	0.10	0.22	3.29
08-02-86	123	8.00	7.09	6.08	4.75	4.98	−0.23	0.90	3.25
08-08-86	113	8.88	6.67	5.11	3.58	3.68	−0.11	2.67	5.76
08-08-86	114	8.88	7.63	6.16	4.29	4.67	−0.38	1.62	4.96
08-08-86	121	8.88	6.59	5.08	3.74	3.59	0.15	2.09	4.94
08-08-86	122	8.88	6.90	5.65	4.34	4.36	−0.02	1.47	4.03
08-08-86	123	8.88	7.04	6.04	4.68	4.99	−0.31	1.14	3.50
08-10-86	113	8.20	7.45	5.71	4.24	3.92	0.32	1.63	4.83
08-10-86	114	8.20	7.72	6.43	4.80	5.04	−0.24	1.07	3.99
08-10-86	121	8.20	7.51	5.93	4.36	4.17	0.19	1.03	4.19
08-10-86	122	8.20	7.59	6.47	5.05	5.18	−0.13	0.58	3.12
08-10-86	123	8.20	7.09	6.10	4.87	4.95	−0.07	0.86	3.08
08-13-86	113	7.90	6.67	5.19	3.96	3.60	0.35	2.04	4.75
08-13-86	114	7.90	7.03	5.77	4.36	4.38	−0.02	1.56	4.23
08-13-86	121	7.90	7.37	5.86	4.18	4.13	0.04	1.17	4.36
08-13-86	122	7.90	7.37	6.04	4.54	4.50	0.05	0.95	3.78
08-13-86	123	7.90	7.54	6.19	4.80	4.58	0.22	0.72	3.47
08-16-86	113	6.43	7.77	5.43	3.60	2.59	1.00	1.14	5.31
08-16-86	114	6.43	7.09	5.92	3.80	4.44	−0.64	1.18	4.46
08-16-86	121	6.43	7.00	5.24	3.40	2.95	0.45	1.12	4.72
08-16-86	122	6.43	10.37	7.89	5.04	4.47	0.58	−0.52	4.80
08-16-86	123	6.43	7.60	6.09	4.19	4.06	0.13	0.61	4.02

was determined. Then the diffusion component was removed from the full model and the dawn DO predictions were generated, using the estimate of the respiration coefficient from the full model application. The overnight net effect of diffusion was defined as the predicted dawn DO for the diffusionless model subtracted from the observed dawn DO. If positive, the net overnight effect of diffusion was an addition of DO to the pond; if negative, the net effect of diffusion was a loss of DO from the pond during the night. The overnight respiration effect was the loss of DO due to the whole pond respiration and was equal to the dusk DO minus the predicted dawn DO for the diffusionless model (see Madenjian et al. 1978b).

Results

Dawn DO forecasts were more accurate for the Amorient site than the MRTC site; the mean absolute value of the residuals for the Amorient site was 0.27 and for MRTC was 0.52 mg $O_2 \cdot L^{-1}$ (Table 1). For both sites pooled, the model prediction, on average, deviated from the actual dawn DO by 0.39 mg $O_2 \cdot L^{-1}$.

Of the 30 trials at Amorient, dawn DO was overestimated by application of the WPRD model in 17 of 30 trials; at MRTC, dawn DO was overestimated in 14 of 30 trials. At Amorient, the model, at worst, underestimated dawn DO by 1.00 mg $O_2 \cdot L^{-1}$ (pond 113 on morning of August 17, 1986) and at best yielded a prediction that overestimated dawn DO by 0.02 mg $O_2 \cdot L^{-1}$ (pond 122 on morning of August 9, 1986) (Table 2). For trials at MRTC, the worst prediction of the WPRD was an underestimation of dawn DO by 1.34 mg $O_2 \cdot L^{-1}$ (pond 10 on morning of October 12, 1986) and at best was within 0.05 mg $O_2 \cdot L^{-1}$ of the actual dawn DO (pond 10 on morning of December 9, 1986) (Table 3).

The regression of actual dawn DO on predicted dawn DO using data from both sites (Amorient and MRTC) pooled yielded a line of slope 0.93 (slope not significantly different from unity, sample t-statistic $= -0.960$, $p = 0.341$) and the intercept was not significant from zero (intercept $= 0.25$, sample t-statistic $= 0.785$, $p = 0.4357$). Hence, there was a 1:1 correspondence between predicted and observed dawn DO (no detectable bias in the predictor) (Fig. 1). Note that the regres-

TABLE 3. Observed and predicted dissolved oxygen concentration (DO) at dawn for MRTC marine shrimp ponds (Hakipuu, Oahu), August through December 1986. Predictions were based on the WPRD model using a DO measurement at dusk and a second DO measurement 3 h after dusk. The diffusion effect (DE, mg $O_2 \cdot L^{-1}$) was the overnight loss (denoted with a negative sign) or gain of DO due to diffusion. The respiration effect (RE, mg $O_2 \cdot L^{-1}$) was the overnight DO loss due to respiration. Date was for start of sampling period.

Date (mo-d-yr)	Pond	Wind speed ($m \cdot s^{-1}$)	Measured DO (mg $O_2 \cdot L^{-1}$)			Predicted dawn DO	Residual	DE	RE
			Dusk	3 h after dusk	Dawn				
08-30-86	7	1.61	12.11	9.57	5.14	5.03	0.11	−0.61	6.37
08-30-86	9	1.61	12.28	9.87	4.65	5.50	−0.85	−0.46	7.17
09-01-86	6	1.40	9.51	7.40	3.33	3.58	−0.25	0.10	6.28
09-01-86	7	1.40	9.65	7.65	4.42	3.89	0.53	−0.11	5.12
09-05-86	6	1.74	13.20	10.97	6.78	6.86	−0.07	−1.11	5.30
09-05-86	9	1.74	12.53	9.53	3.17	3.66	−0.49	−0.25	9.11
09-07-86	6	1.49	11.23	9.05	4.31	5.01	−0.70	−0.31	6.62
09-07-86	7	1.49	11.16	8.70	3.65	3.98	−0.33	−0.18	7.33
09-07-86	9	1.49	10.72	8.12	3.05	2.93	0.12	−0.02	7.65
09-07-86	10	1.49	11.81	9.05	3.55	3.66	−0.11	−0.24	8.02
09-08-86	6	1.34	10.88	8.37	3.40	3.94	−0.54	−0.12	7.36
09-08-86	7	1.34	10.55	7.85	2.16	2.98	−0.81	0.10	8.48
09-08-86	9	1.34	10.90	8.30	4.26	3.31	0.96	−0.19	6.45
09-08-86	10	1.34	10.54	8.06	3.91	3.48	0.43	−0.13	6.50
09-10-86	6	1.36	13.36	10.86	5.28	6.06	−0.78	−0.75	7.34
09-19-86	7	1.59	10.25	7.54	3.51	2.31	1.20	0.00	6.74
09-21-86	7	1.73	10.29	8.12	2.90	3.43	−0.53	0.10	7.50
09-23-86	6	1.53	12.88	10.58	6.19	5.86	0.32	−0.83	5.87
10-07-86	6	1.39	12.86	10.35	5.56	5.16	0.40	−0.43	6.87
10-07-86	10	1.39	8.47	6.27	2.93	2.10	0.83	0.43	5.97
10-11-86	6	1.37	12.78	10.17	5.19	4.53	0.65	−0.40	7.19
10-11-86	10	1.37	11.68	9.04	5.22	3.88	1.34	−0.35	6.11
10-13-86	6	1.42	10.88	8.34	3.38	2.96	0.42	0.06	7.57
10-13-86	10	1.42	9.93	7.86	3.56	3.51	0.05	0.16	6.53
10-14-86	6	1.45	10.67	8.51	4.01	3.83	0.18	0.01	6.68
10-14-86	10	1.45	9.81	7.81	3.56	3.67	−0.11	0.18	6.43
11-02-86	9	1.39	10.57	8.06	4.17	3.07	1.10	0.01	6.41
11-04-86	10	1.47	10.76	8.38	2.87	3.28	−0.40	0.22	8.11
12-08-86	7	1.39	13.62	10.77	5.87	5.03	0.84	−0.33	7.42
12-08-86	10	1.39	11.55	9.42	4.36	4.41	−0.05	0.05	7.25

sion lines for each site separately did not differ significantly; the regression for pooled data is presented.

The predicted nighttime DO curve (based on an observation at dusk and another observation 3 h later) for pond 7 from August 30 through August 31, 1986, closely matched the observed DO curve (Fig. 2). The predicted DO was slightly less (about 0.3 mg $O_2 \cdot L^{-1}$ less) than the observed DO from about 2330 to 0500.

The net diffusion effect at Amorient ranged from a modest depletion of DO of 0.52 mg $O_2 \cdot L^{-1}$ during the night beginning on August 16, 1986, in pond 122 to a substantial input of DO of 4.12 mg $O_2 \cdot L^{-1}$ in pond 121 on the night of July 26, 1986 (Table 2). On the average, the net effect of diffusion in Amorient ponds was an addition of 1.28 mg $O_2 \cdot L^{-1}$ during the night (Table 4). In contrast, a depletion of 0.18 mg $O_2 \cdot L^{-1}$ was the average overnight net effect of diffusion to DO in the MRTC ponds. Average nightly wind speeds during the trials at Amorient ranged from 6.43 to 10.07 $m \cdot s^{-1}$; the MRTC site was subjected to considerably less wind as wind speeds averaged between 1 and 2 $m \cdot s^{-1}$ at night during the trials.

Discussion

The WPRD model accurately predicted dawn DO at Amorient and MRTC marine shrimp ponds. Conditions ranged widely during the validation period for whole pond respiration rate, dusk DO, and wind speed. The model appeared appropriate for brackish-water as well as freshwater ponds. The relationship of the oxygen diffusion coefficient as a function of wind speed, described by Banks and Herrera (1977) and used by Madenjian et al. (1987b) for freshwater prawn ponds, appeared to work well for brackish-water ponds also.

The WPRD model has been verified for well-mixed brackish-water ponds. However, it has also been verified for freshwater

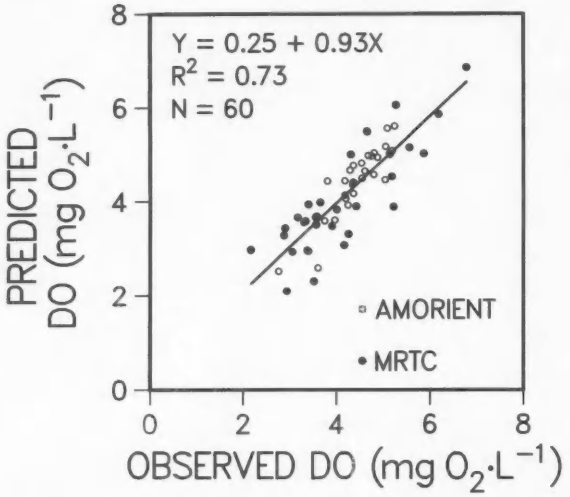

FIG. 1. Predicted vs. observed pond DO at dawn for Amorient ponds (Kahuku, Oahu) and MRTC (Hakipuu, Oahu) ponds, July through December 1986. Predicted dawn DO was based on the WPRD model using a 3-h lag between the dusk and second DO measurement.

ponds that have shown DO stratification early in the evening but that destratified quickly during the night. Whether the model adequately predicts dawn DO in ponds that remain stratified throughout the night has not yet been shown. Seasonality has had no effect on the model success, since the model has furnished accurate predictions of early morning DO year round. We expect successful application of the WPRD method in other geographical regions, provided there are no extreme changes in respiration rate or wind speed in the middle of the night. Furthermore, we expect the method to perform well in ponds of various depths and shapes. The model would have to be modified to accomodate ponds into which there was an appreciable inflow of water.

The predictions of the WPRD model were more accurate (smaller mean absolute value of the residuals) for the shrimp ponds at Amorient than the shrimp ponds at MRTC. MRTC ponds were sampled at only one location, while two locations were sampled at each of the Amorient ponds. Madenjian et al. (1987b) found that predictions based on sampling at just the west station of Amorient prawn ponds were as accurate as predictions based on data from both east and west stations of the pond. However, predictions based solely on observations at the east station of the ponds were less accurate than either predictions based on an east–west average or predictions based solely on observations from the west station. Thus, there was an indication that sampling from one station could lead to less accurate predictions than those based on observations from two different stations on the pond.

Our results contradict the postulation of Pruder (1986) that the effect of diffusion is inconsequential in DO dynamics of aquaculture ponds. The importance of diffusion was particularly evident at the Amorient site, where the net overnight effect of diffusion exceeded one third of the whole pond respiration effect in 10 of 30 trials. The diffusion effect was considerably more important at the Amorient shrimp ponds than at the MRTC shrimp ponds. The Amorient site was windier (average observed nightly wind speed of 8.25 $m \cdot s^{-1}$ during the study opposed to 1.27 $m \cdot s^{-1}$ at MRTC) and hence the rate of oxygen transfer between the atmosphere and pond water was greater than that for the MRTC facility.

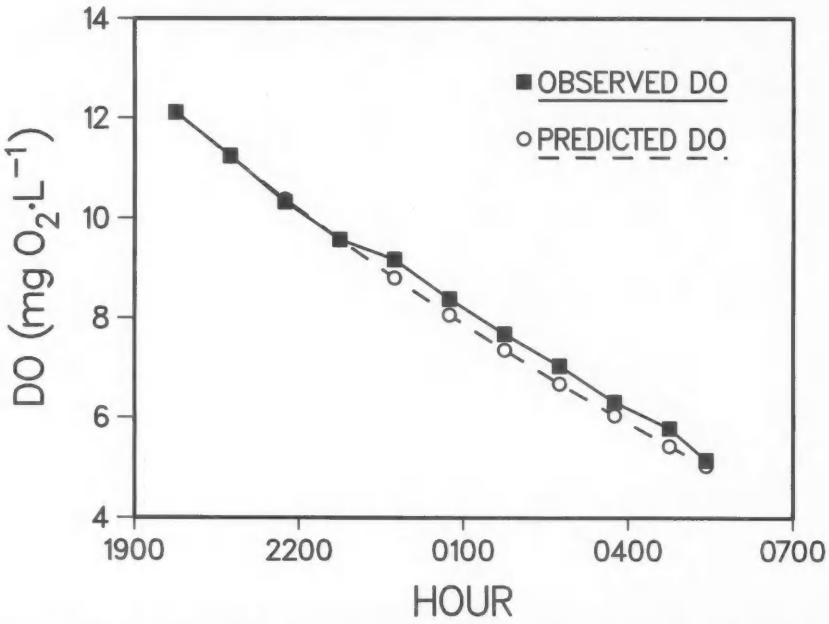

FIG. 2. Observed and predicted pond DO at MRTC pond 7 (Hakipuu, Oahu) during the night beginning on August 30, 1986. Predicted DO was based on the WPRD model using DO observations at 1935 and 2235.

TABLE 4. Minimum (min.), maximum (max.), and mean (standard error) of the net overnight diffusion effect (DE) for marine shrimp ponds at Amorient (Kahuku, Oahu), July through August 1986, and at MRTC (Hakipuu, Oahu), August through December 1986. DE represents the increase in pond DO due to diffusion of oxygen from the atmosphere into the pond during the night. A positive DE signifies that the net overnight effect of diffusion was to add oxygen to the pond from the atmosphere, while a negative DE signifies that the net overnight effect of DO was to remove oxygen from the pond. See text for description of how DE was calculated. N = number of trials.

		DE (mg $O_2 \cdot L^{-1}$)		
Site	N	Min.	Max.	Mean (SE)
Amorient	30	−0.52	4.12	1.28 (0.18)
MRTC	30	−1.11	0.43	−0.18 (0.06)
Amorient and MRTC pooled	60	−1.11	4.12	0.55 (0.13)

In summary, the WPRD model yielded accurate predictions of dawn DO in the marine shrimp ponds of Amorient (Kahuku) and of the MRTC farm (Hakipuu) on Oahu, Hawaii. The model was validated for a wide range of wind speeds from about 1 $m \cdot s^{-1}$ to over 10 $m \cdot s^{-1}$. Since the WPRD model previously was verified for freshwater ponds, we propose that this technique can be widely applied to aquaculture ponds. Diffusion of oxygen by wind reaeration into the ponds at Amorient was an important factor for the observed nighttime DO decline.

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PERSPECTIVES

Is Research on Environmental Factors Useful to Fisheries Management?

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The study of environmental effects on fish distributions and recruitment rates has become a major research focus with substantial funding. This research is justified by rather vague claims about understanding the causes of variability and making more accurate predictions based on this understanding, claims which often do not bear close inspection. Improved prediction is often impossible in principle because environmental factors are not predictable even if fish responses are. In some fisheries, prediction could be achieved more cheaply and reliably by direct monitoring programs such as precruitment surveys of year-class strengths. In others, prediction is unnecessary because of existing feedback tactics for regulation, or would be primarily valuable to particular industrial interest groups and hence should not necessarily be subsidized by public research investment. Better understanding is needed for situations in which the effects of environmental factors are confounded with the effects of stock size and fishing. In these cases the key uncertainties will not be resolved by continued correlative and biological process studies and will instead require bold management experiments in which environmental studies are coupled with deliberate manipulation of stock sizes through changes in harvest policies.

L'étude des effets environnementaux sur la distribution et le taux de recrutement des poissons est devenu un important sujet de recherche auquel on consacre d'importantes sommes. Ces travaux de recherche sont justifiés par des allégations plutôt vagues relativement à la connaissance des causes de la variabilité et à la formulation de prévisions plus précises fondées sur ces connaissances, allégations qui souvent ne sont pas justifiées. Il est souvent impossible en principe d'améliorer les prévisions parce qu'il est impossible de prévoir les facteurs environnementaux même si les réactions des poissons le sont. Dans le cas de certaines pêches, les prévisions peuvent être faites à un coût moindre et avec plus de fiabilité au moyen de programmes de surveillance directe comme des campagnes de pré-recrutement des effectifs de la classe annuelle. Dans le cas d'autres pêches, les prévisions ne sont pas nécessaires en raison des tactiques de rétroaction existantes en matière de réglementation, ou elles ne seraient surtout valables que pour des groupes ayant des intérêts industriels donnés et ne devraient pas nécessairement être subventionnées par des investissements publics en matière de recherche. Une meilleure compréhension est nécessaire dans les cas où les effets des facteurs environnementaux sont confondus avec les effets de l'effectif et de la pêche. Dans ces cas, les incertitudes clés ne seront pas résolues par des études de corrélation et des processus biologiques, et il faudra plutôt effectuer des expériences de gestion dans le cadre desquelles des études environnementales sont couplées à une manipulation délibérée des effectifs par le biais de modifications des politiques de capture.

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It is a truism that fish production ultimately depends on physical factors such as water transport and temperature, and there is little doubt that variation in these factors is somehow involved in the fluctuations that most stocks exhibit. If for no other reason than pure scientific curiosity, fisheries scientists should be concerned with understanding the physiological, behavioral, and ecological linkages through which environmental factors influence recruitment rates and distribution patterns. However, research on environmental effects on fish populations is often justified by its potential economic value for fisheries management (e.g. improved predictions of recruitment), and depends on management to create or permit informative variation in stock sizes over time. Considering this interdependence, it is important for researchers to be precise about just what they can accomplish, whether their contributions might be enhanced or obtained more cheaply by other means (such as prerecruitment index monitoring of year-class strengths), and the extent to which management experiments can enhance or confound their research results.

This paper reviews alternative management strategies for dealing with recruitment variability, asks what predictions are needed under each strategy and how to obtain these predictions most cheaply and reliably, and comments on whether existing research approaches are likely to provide the predictive models that are needed. To stimulate further debate on these topics, we take a deliberately provocative viewpoint, arguing that (1) better

prediction is much less important today than better monitoring and feedback strategies and (2) even where prediction is needed, existing research approaches are incapable, even in principle, of meeting that need.

Management Strategies for Dealing with Variability

Fisheries managers have many responsibilities, ranging from resource conservation and enhancement to economic planning for marketing fish and preventing industrial overcapitalization. In most cases the chief responsibility is to regulate harvest to insure future productivity (conservation); this essay focuses on that concern. There is a substantial literature on how harvest rates should be adjusted over time in response to natural variability, particularly in recruitment rates (reviews in Clark 1985; Mangel 1985; Vincent et al. 1987; Walters 1984, 1986). In general the best policy involves some feedback relationship between harvest rate and stock size, such that catches are regulated up and down in response to natural variability, to maintain a fairly stable escapement (stock after harvest) each year.

If short-term variations can be accurately forecast, the best policy may be to adjust the target stock size so as to increase catch when positive variation is anticipated and to reduce when negative. If variation is unpredictable, the best feedback policy can be computed without knowing the biological causes of variability, and this policy is quite insensitive to the exact statistical distribution of the variability, unless it involves very long-term climatic cycles. When there are long-term, slow changes, the best policy is generally to assume that the current environmental conditions will persist indefinitely until the data indicate otherwise (Walters 1987).

Fishery managers have long recognized the need to respond to variability, and have evolved three strategies for monitoring and rapid adjustment of regulations. We call these strategies seasonal, annual, and negotiated feedback. The shorter the feedback time, the more monitoring and less prediction is required, as discussed in the following subsections.

Seasonal Feedback Strategy

In some major fisheries, particularly for migratory salmonids, within-season monitoring allows rapid reestimation of stock size and escapement, and correspondingly rapid changes in harvest regulations. Although seasonal feedback strategies can cause considerable economic uncertainty and hardship for fishermen and fish processors, they are quite successful at meeting conservation objectives even when large (two- to four-fold), unpredicted interannual variations in stock size occur. Seasonal feedback strategies do not depend on good preseason estimates of stock size (Buckingham and Walters 1975; Schnute and Sibert 1983), although they can fail embarrassingly when extreme variations occur. Their performance is much more sensitive to having good preseason assessments of the timing and spatial distribution of fish availability — is it a big run with normal timing, or a small one coming early? — and to having clear, long-term escapement targets defined by the average relationship between stock size and recruitment.

What is the most efficient way in seasonal feedback fisheries to obtain early assessments of timing and distribution, and whether an extreme stock size is in the offing? Here the manager has a choice: (1) develop predictions based on correlative information (oceanographic conditions, juvenile abundances, etc.) or (2) organize the timing and location of monitoring programs to provide abundance, distribution, and timing information shortly before key decisions have to be made. Obviously a combination of these approaches may be best, but at present the poor track record for prediction should lead most managers to emphasize the monitoring approach. In many cases an effective "early warning" monitoring system could be developed at minimal cost to the management agency by allocating part of the allowable catch to test fishing licenses that are restricted to particular, informative times and places, and are still highly profitable.

Improved pre- and in-season monitoring programs and studies of fish–environment relationships are not necessarily competing investments. Indeed, monitoring programs aimed initially at management needs may provide better long-term data for research studies than could ever be obtained by independent researchers.

Annual Feedback Strategy

If seasonal regulation changes are impractical, unnecessary, or economically burdensome, then regulation changes (total allowable catches, season length, etc.) are made on a year-to-year basis with the regulations for each year announced well before the fishing season. Such annual feedback strategies are used in the majority of North American fisheries, both sport and commercial, marine and freshwater. Annual feedback can fail if efficient fishermen pursue highly variable stocks consisting of only one or a few age-classes of fish, such as Pacific salmon. These cases require better year-to-year predictions, or a seasonal feedback strategy. Annual feedback strategies are best applied to long-lived species with multiple year-classes, in which year-to-year recruitment variation does not strongly affect (or rarely affects) the total stock size. In these cases, short-term predictions of year-class variation within 50% or so of the average recruitment rate would have little impact on the annual process of changing regulations to maintain overall target stock sizes.

If it is extreme events that really matter to annual feedback management, the question again becomes what is the best way to anticipate the extremes, at least the year before they affect the stock? As in seasonal management, there are two basic options: (1) predict the extremes from environmental factors and/or (2) monitor recruitment changes through changes in relative abundance of prerecruits. The search for predictive models is hampered by the rarity of the events to be predicted; very long time series are needed before enough events are seen. On the other hand, monitoring prerecruitment abundance or indices of year-class strength directly often requires considerable expense for rather imprecise estimates. Either investment is risky, and the best approach may be to search diligently for index information from other sources, such as the discard rate of prerecruits by other fisheries.

Recruitment rates tend to be lognormally distributed with many average or below-average years punctuated with occasional strong year-classes (Hennemuth et al. 1980). This is consistent with the hypothesis that recruitment is the product of survival rates over several independent life stages, all of which must be high to produce a strong year-class in a given year. Any single environmental factor will probably affect only one of the survival rates, and a manager using this environmental factor will be able to predict some of the average or below-average years but none of the strong year-classes. (For examples of this pattern between recruitment and single environ-

mental correlates, see Myers and Drinkwater 1988).) The search for single causal mechanisms is likely to be misleading (Shepherd et al. 1984); several, perhaps many, environmental correlates would be required to predict strong year-classes.

Negotiated Feedback Strategy

For some fisheries it has not been economically or politically feasible to change harvest regulations from year to year, and substantial change requires a long period of argument and negotiation. For example, the current Canada–U.S. Pacific salmon treaty sets regional quotas on chinook salmon (*Oncorhynchus tshawytscha*) and defines a negotiation process for changing the quotas. This process includes technical analyses that may be disputed by parties interested in preventing short-term change. The presence of quotas encourages regional managers to "meet the target," even when local data indicate that more restrictive regulations are needed.

Negotiated feedback strategies are pathologically poor when efficient fishermen pursue highly variable stocks, and the problems will not be alleviated by better short-term predictions. Such predictions will not be believed, or would not matter anyway, to parties with myopic interests. In these cases the need for better prediction is less than the need for a more flexible feedback strategy with improved monitoring, authority to make rapid changes, and economic investments to increase industrial flexibility (Walters 1984).

Long-term predictions of climatic change would be extremely valuable to managers in negotiated feedback situations. Such predictions could be used to plan ahead for major regulatory changes (number of licenses, etc.) if managers also could reduce catches during periods of low abundance. Fishery managers should develop this flexibility as a top priority — whether or not better predictions are obtainable.

Information Needs for Setting Stock-Size Targets

We noted in the previous section that feedback policies for dealing with unpredictable variation can be constructed without knowing the causes of the variation. Once the statistical properties of the variation are specified, the same policy will be optimal no matter what the cause. It can in fact be quite misleading to base policy on a model that simulates the causal effect of variation of a particular environmental factor on future stock sizes. Such a model may dangerously underestimate variability due to other factors; adding additional variability to account for such factors would be equivalent to using the overall variability directly, without reference to any environmental submodels. A good feedback policy requires (1) an adequate statistical description of variability and (2) an accurate description of the mean relationship between stock size and surplus production or the components of production (recruitment, growth) on which management decisions are based.

To what extent can better understanding of environmental factors help meet these requirements? Obviously if we knew precisely (quantitatively) how a particular environmental factor influences production rates, we could use data on that factor to "filter out" part of the variability in historical data and thereby get a clearer picture of the underlying mean effect of stock size (Shepherd et al. 1984). However, we are not given such quantitative relationships in advance; we have only historical records containing mixed effects of environment and stock size, with no knowledge of even the correct functional form to assume between production and each factor, let alone which environmental factors are important in the first place. In this case it is meaningless or even misleading to filter the production (or recruitment) data using environmental correlates, especially if the stock size has not been deliberately manipulated so as to provide a clearly contrasting set of levels for each level of the environmental variates — which is a practical impossibility anyway.

Assessing stock size versus environmental effects from historical data can be particularly misleading if there is a possibiliy of cyclic environmental effects with periods roughly twice the mean fish generation time (Botsford 1986; Koslow et al. 1987). By simulating data under these conditions, Armstrong and Shelton (1988) found that the estimated stock–recruitment relationship was more dome-shaped than the known curve and the error variance was underestimated. Given these conditions, a plot of recruitment versus stock size (Fig. 1a) has a negative slope that may be interpreted as the descending limb of a Ricker stock–recruitment relationship, which implies that high fishing rates would result in a stable low stock size with high recruitment rate. (For examples of apparently negative stock–recruitment relationships, see the analyses of Arcto–Norwegian cod (*Gadus morhua*) (Garrod 1967) and Pacific halibut (*Hippoglossus stenolepis*) (Mundy et al. 1985).) However the same data could be caused by cyclic deviations (Fig. 1b) from a Beverton–Holt stock–recruitment relationship, which would imply that high harvest rates will cause disastrous stock declines when the environmental effect is negative.

This confounding of stock size and environmental effects is an extreme case of the time-series bias noted by Walters (1985). Apparently negative stock–recruitment relationships can arise when favorable environmental conditions cause stock size to increase, but with a lag such that the stock is high by the time the environmental effects deteriorate. Such confounding can only be broken by deliberately changing fishing patterns or by a lucky sequence of events; for example, North Sea gadoid stocks increased in the 1960s despite heavy fishing (Cushing 1984).

Long-term environmental changes can confound efforts to estimate the average effects of stock size, while year-to-year "noise" just makes the averages a bit harder to see. Understanding how environmental changes affect fish productivity would be very valuable to fishery management, but it may take decades to observe the effects, and stock-size changes may continue to be confounded with these effects. Such understanding may thus be unobtainable unless fish populations are deliberately managed to break up the potential stock–environment correlations.

Predictions for Fishing Industries

Is research on the causes and correlates of variability justified simply by its value to fishing industries, even if it is not critical for conservation management? While feedback management strategies can optimize productivity and achieve basic conservation goals without good predictions, such strategies are likely to exaggerate the variability and uncertainty in catches by fishermen and supplies to processors. Using Skeena River sockeye salmon (*Oncorhynchus nerka*) as an example, Walters (1975) found that higher mean catches can be obtained only at the cost of increased variance in catch.

Would individual fishermen benefit from good short-term (1- to 5-yr) predictions? We believe the answer is a resounding no,

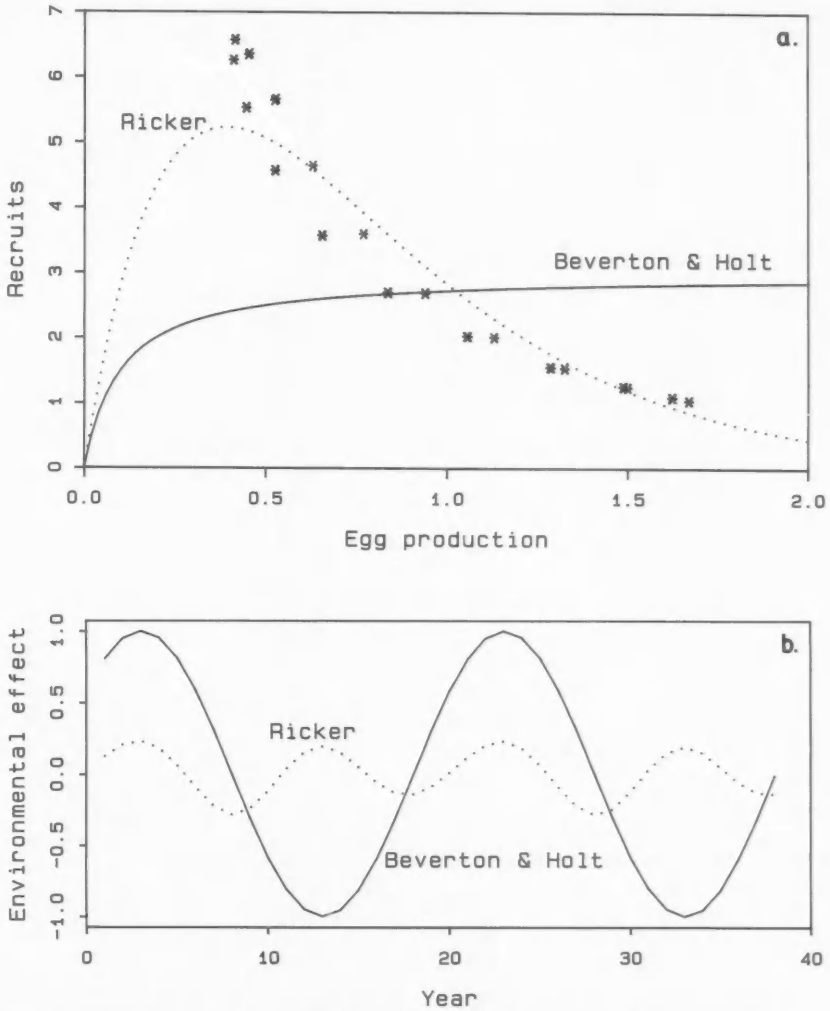

FIG. 1. (a) Stock–recruitment data generated with an age-structured model designed to simulate the population dynamics of Pacific halibut (*Hippoglossus stenolepis*). (b) Cyclic environmental variables that are assumed to exert a multiplicative effect on recruitment. The simulated stock–recruitment data were actually generated from the Beverton–Holt curve with the 20-yr period deviations, although the Ricker curve with 10-yr period deviations seems to fit much better.

for the obvious reason that one of a fisherman's main concerns and sources of unpredictability is the behavior of other fishermen. This is especially true because of the overcapitalization that characterizes most North American fisheries. Each fisherman must guess how the others will respond to the better predictions of fish abundance and distributions that would presumably result from public research programs. Currently he can count on others spreading their activities in time and space, due to unpredictability, but with better predictions he could reasonably expect worse crowding and overreponse to investment opportunities. In short, his own planning might be even more difficult than it is now. Forecasts would be useful to individual fishermen who worked cooperatively or operated under individual quotas to avoid interference. While such arrangements are being considered in Atlantic Canada, they are unlikely to develop in most North American fisheries in the foreseeable future.

Fish processors, tourist facility operators, and developers in sport fisheries are much more likely to benefit from short-term predictions than are commercial fishermen, particularly in planning major capital investments and market development. Here we face the thorny political issue of whether it is proper or necessary for public agencies to subsidize private investment planning. We have no arguments to offer on that issue, but warn fisheries investigators that they may have to confront it in attempts to justify the development of better forecasting models. In Atlantic Canada the government has invested in the major fishing companies to ensure their continuing viability, and also produces 5-yr forecasts of population and yield trends to aid industry planning. In other areas, commercial fishing compa-

nies may choose to directly fund research on short-term predictions.

Adequacy of Existing Research Approaches

In the previous sections we argued that better understanding and predictive models are badly needed, but that these needs can be met more cheaply by improved monitoring programs in most management situations. Monitoring programs are insufficient in situations involving the effects of long-term environmental variability, which confuses the calculation of target stock sizes, and for which it may be necessary to plan ahead to make major regulatory changes. Existing research approaches mainly involve correlative studies on historical data, or detailed, biophysical process studies in local areas where critical life-history processes are thought to unfold. Are these approaches likely to produce the predictive models that are needed, especially to cope with long-term environmental variability?

Correlative Approach as a Way to Misdirect Research

The fisheries literature has recently been flooded with correlative studies purporting to show how recruitment rates are related to various environmental factors. Each study generally contains a nice rationalization of the mechanism for the correlation as well as the usual litany of warnings about the risk of spurious correlation and how the results should be viewed only as a starting point for further research. There is seldom an honest appraisal of how easy it is to rationalize any correlation, how large the risks really are of reporting a spurious correlation, and what further research should entail.

The risk of spurious correlation cannot be assessed by statistical analysis of a given data set, beyond the standard measure of "by chance alone" provided by significance levels. Some experience suggests that the risk is much higher than indicated by standard significance tests. For example, there is a long tradition of correlative studies on variation in Pacific salmon abundance, for which there are very obvious freshwater environmental factors such as stream flows that should have some influence on recruitment, and also some obvious oceanographic factors such as coastal current patterns. However, as far as we are aware, none of these correlations has stood the test of time; in fact, it is a standard joke among salmon investigators that "the model worked well until next year." The amazing thing is not that the correlations break down with such disturbing regularity, but that apparently sensible scientists keep searching for them.

It is entirely too easy to find spurious correlations. Given that a recruitment time series is very likely to have strong autocorrelations, and that many environmental time series also have some autocorrelation structure, one need scan only a few of these series before finding a "significant" correlation. If you do not believe this, simulate a dozen or so random environmental time series with a lag 1 autocorrelation coefficient of around 0.5 and compare these series with real recruitment data. Significance tests are meaningless when exploratory scanning precedes the final test calculation (as is almost always the case), and most investigators do not even count how many environmental series they have examined.

Supposedly, the risk of spurious correlation can be reduced by dividing the data into fit and prediction sets and then seeing which correlations in the fit set also hold in the prediction set. This is absurd: the investigator can simply scan until finding a correlation that does hold up over both sets and then report only this finding; the result is exactly the same as if he had fit both sets in the first place, and the risk of a spurious correlation is identical. The acid test of recruitment–environment correlations is the ability to forecast data not available at the time of the original analysis (Shepherd et al. 1984). Drinkwater and Myers (1987) reanalyzed correlations between environmental variables and catches of several Gulf of St. Lawrence and Gulf of Maine fishes. None of the correlations remained significant after accounting for the loss of degrees of freedom due to the high autocorrelation of the data.

Fisheries is in much the same position today as was disease research in the middle of the nineteenth century, when Robert Koch first demonstrated how to distinguish real pathogens from other microorganisms spuriously correlated with disease. We lack the experimental control to apply Koch's famous postulates for reproducibility of results to fish populations, but we should at least insist on a few basic precautions: (1) report all data sets (number, type, lags tried) scanned during a search for correlations, (2) do not report biological rationalizations unless they can be supported by a variety of independent measurements, and (3) report any evidence, especially negative, about whether the correlation holds for the same species in other areas or other species in same area. By biological rationalization, we mean demonstrating a plausible causal mechanism (collection of physical and biological interactions) for the correlation; several such mechanisms are always possible for any complex ecosystem, and there are always reasons why the rationalization may not hold for other stocks or areas. In the case of long-term climate cycles, "common wisdom holds that proof [of a correlation] requires six well-behaved cycles, especially when there is no well-known mechanism" (Kerr 1987).

Detailed Biophysical Studies

Various resource agencies have undertaken substantial oceanographic and limnological studies of particular areas (sometimes mislabelled "experiments") to investigate the effect of environmental factors on fish populations, particularly the larval and juvenile life stages. These studies are producing fascinating insights into how fish respond to small-scale environmental variation. Such studies generally do not cover the full spatial distribution or life span of the species under study, but it is presumed that variability on those larger scales involves localized "critical events," the effects of which can be measured and will persist on the larger scales.

Suppose a detailed study reveals a striking correlation between survival and some physical factor, and the mechanism for the correlation is so obvious and well documented that there is no question about spurious correlation or alternative mechanisms. Consider, for example, the negative relationship between survival of larval anchovy (*Engraulis mordax*) and wind speed (Peterman and Bradford 1987). Should a fishery manager assume that a predictive model based on this mechanism is correct and directly applicable to the larger spatial scale and whole life cycle for which he is responsible, and over which he must try to interpret patterns in historical data? The answer is generally no, because the model would involve a gross extrapolation beyond the circumstances encountered in the local study. In the anchovy example, larval survival is not correlated with recruitment at age 1 (Peterman and Bradford 1988).

A detailed, process-oriented study can only provide a model or testable hypothesis about causes and patterns of overall var-

iability. In this respect, it is the same as a crude correlative study based on historical data. Just as a correlative study can fail due to spurious correlations or events occurring outside the range of historical experience, predictions based on a process-oriented study can fail due to events outside the space–time–environmental "window" of that study. In both cases the ultimate test of the predictions is hard experience, gained at the frustratingly slow rate of one observation per year; gathering lots of detailed environmental data cannot in principle substitute for that experience. Thus the detailed studies face two risks: choosing an inappropriate study window in which no obvious local correlation emerges from the analysis, or finding strong local effects but having these reversed or cancelled at larger space–time scales. These risks alone do not mean that detailed studies are a waste of time: they may ultimately prove very useful and have considerable curiosity value. But we should not pretend that they represent a major step beyond simpler correlative studies, at least in their value for fishery management.

Integration of Research and Management

The answer to the question posed in our title is yes, but a qualified yes. We readily acknowledge that conventional environmental studies bear directly on practical problems other than predicting fish distributions and recruitment. Limnologists have the water quality problem, which has a strong environmental component, while oceanographers are concerned with global geochemical processes such as CO_2 pathways. In addition, research on environmental factors may contribute to fisheries management in novel ways, for example, through the enhancement of the natural productivity of fish populations by fertilization and predator control.

To date, environment–fish studies have been more successful in predicting fish distributions than recruitments. This is not surprising — fishes have known physical (e.g. temperature) preferences whereas recruitment is a product of many events during early life. Knowledge of environmental effects on fish distributions could be used to improve estimates of abundance in long-term monitoring programs (Pinhorn and Halliday 1985). Many of our arguments are more relevant to predicting fish productivity than to predicting fish distributions. However, in analyzing recruitment data from coastal fisheries that do not exploit the entire geographic range of the stock, variability in production is often indistinguishable from distribution changes.

In justifying their research to resource agencies (which increasingly seek more direct returns on research investments), fisheries scientists must specify more explicitly how their results will be used. Environment–fish correlations and detailed biophysical studies are useful for generating hypotheses, but deliberate experiments are required to test these hypotheses. Management experiments coupled with long-term monitoring may not sound very exciting but they are more scientifically defensible than "just so" rationalizations of environmental correlations.

We noted earlier that fishery managers might profit more from investing in better monitoring programs than in research aimed at uncovering the causes of variability, and that such monitoring may contribute to better research studies as well. The development and testing of improved monitoring schemes is an important area for collaboration between researchers and managers. However, this integration will have to extend much further than at present if we are to eventually understand the interplay between stock size and environment as determinants of productivity.

Identifying long-term, target stock sizes from the average effects of stock size on production is critical for designing feedback management strategies for dealing with variability, predictable or not. The target stock size must be based on historical experience of how stocks actually perform, and the assessment can be misleading due to confounding of environmental and stock-size effects. This confounding has led to bitter arguments among fisheries scientists, such as the famous "Thompson–Burkenroad debate" about Pacific halibut (Skud 1975); these arguments will not be resolved by continuing to manage fisheries so as to leave the effects confounded, no matter how many studies lend plausibility to particular arguments. Distinguishing the effects will require bold and deliberate experiments to establish contrasting stock sizes — the only variables that can be "controlled." These experiments must involve both management and research changes.

In the Pacific halibut example (Mundy et al. 1985), historical data are consistent with two very different models: a dome-shaped stock–recruitment curve, such that heavy fishing would result in sustained high recruitment, and a cyclic response to climatic change, such that heavy fishing would soon result in a major decline (Fig. 1). We could discriminate between these alternatives by performing an ecological "press experiment" (Bender et al. 1984): liberalize the fishing regulations now, while the stock is increasing, and see what happens during the next 20 yr. Economically and ecologically, this would be a very dangerous experiment. In such cases, we may have to admit that it is presently too risky to resolve the uncertainty, and that we may have to live with uncertainty into the foreseeable future. Having made this admission, we should not waste further research money on environmental studies that could not, in principle, untangle the confounded effects.

Fortunately, there are many cases in which stock-size manipulation experiments could be performed, in conjunction with studies of environmental factors, on species living in spatially discrete subpopulations. In these cases, the risks of overfishing in press experiments and lost income due to reduced fishing can be isolated on a few subpopulations, and valuable "control" information about climatic effects can be obtained from non-manipulated subpopulations. Such an experiment has been proposed for slope rockfish off the British Columbia coast (Walters and Collie 1989), another is underway off the west coast of Australia (Sainsbury 1988), and several have been tried or contemplated for various Pacific salmon stocks.

There is a fundamental difference between deliberate, experimental management and conservative management that waits, hoping for natural events to create the contrasting circumstances needed to distinguish environmental and stock-size effects. Waiting and hoping could require decades or even centuries to resolve long-term climatic effects, and there is no use pretending that short-term correlative or process studies will allow us to extrapolate to longer time scales. It would be foolish to claim that either the experimental or the waiting approach is always best; the choice has to be made on a case-by-case basis, using careful risk assessment and economic analysis. The challenge now is to develop imaginative plans integrating environmental studies, monitoring, and experimental harvest manipulation and to carry out the objective analyses needed to decide whether these plans should be implemented in the field.

Acknowledgments

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LETTERS AND COMMENTS/ LETTRES ET COMMENTAIRES

About Carcinogens and Tumors

In a recent paper, Geraci et al. (1987) reviewed tumors in cetaceans and discussed questionable diagnoses that, in the words of the authors, have had a tendency to become established as facts through successive publications. We wish to comment on their dismissal of a proposed interpretation for the aetiology of a bladder cancer reported from a beluga whale (*Delphinapterus leucas*) from the St. Lawrence (Martineau et al. 1985). Geraci et al. (1987) wrote that the suggestion that this carcinoma could have originated from benzo[a]pyrene (BaP) exposure was a "simplistic attempt to link environmental polycyclic aromatic hydrocarbons…in an environment in which concentrations of [these compounds] are not particularly high."

Ironically, Geraci et al. (1987) cited the same sources as we did to support their claim that polycyclic aromatic hydrocarbon (PAH) contamination is not high in the St. Lawrence beluga environment. These studies, however, unequivocally indicate that there are large amounts of PAHs in the Saguenay fjord, in the heart of the habitat of the resident population of beluga whales. Martel et al. (1986) evidenced large amounts of PAHs spread over an 80-km stretch of the fjord. Chromatograms and sediment profiles as well as regional comparisons showed that the dominant source was anthropogenic, originating from nearby aluminium smelting plants that have been operating since the late 1930s. Accumulation in sediments could be traced through the last 30–60 yr, mostly from liquid effluents until 1976, and presently from atmospheric fallout. Nearest to the plants, PAH concentration in sediments reach 3.8 ppm. The above study also highlighted a strong hydrodynamic element to the distribution of PAHs downstream towards the St. Lawrence.

BaPs are a major component of this burden and their total release into the environment by smelting plants along the Saguenay has been estimated at 20 tons·yr^{-1} (Picard-Bérubé and Cossa 1983). Furthermore, these authors have demonstrated the bioavailability of BaP to marine organisms in the area. Very high levels of BaP (average of 26 μg·kg^{-1} dry weight) were found in blue mussels (*Mytilus edulis*) living at the Saguenay mouth. Similar mussels transplanted from clean areas to various sites along the fjord increased their initial BaP levels at least 200 times (to 32 μg·g^{-1} dry weight) within 1 mo. BaP is recognized as one of the most potent carcinogen chemicals known (Heidelberger 1975; Cheville 1983). Uptake and/or accumulation of BaP by various aquatic and marine invertebrates (Payne 1977; Vandermeulen and Penrose 1978; Dunn and Fee 1979; Uthe and Musial 1986) and vertebrates (Lee et al. 1972; Spacie et al. 1983) and binding of BaP metabolites to DNA and protein in exposed mammals (Bernard et al. 1983; Stowers and Anderson 1984) leading to carcinomas have been well documented.

St. Lawrence beluga whales live for up to 30+ yr and have a varied diet of pelagic, demersal, and benthic organisms at various trophic levels, even ingurgitating sediments (Vladykov 1946). As belugas intensively use the lower part of the Saguenay and adjacent St. Lawrence waters, they evidently are exposed to sediments and organisms contaminated with BaP. This compound was not, however, detected in various tissues of the whale with a bladder cancer (Martineau et al. 1985). We rationalized this result on the basis of metabolic considerations, but analytical methods may also have been inadequate in this particular case. More recent analyses of brain tissues from three other adult animals chosen randomly indeed demonstrated the presence of BaP adducts in the DNA of the brains of all three animals (Martineau et al. 1988); a control sample from Arctic animals contained no adducts (Shugart et al. 1987). This provided incontrovertible evidence that the St. Lawrence animals had been exposed to BaP and had metabolized it to the "ultimate" carcinogenic form, the diolepoxide (BaPDE), which subsequently became covalently bound to the DNA of brain tissue (Martineau et al. 1988). Levels approach that found in laboratory animals exposed to carcinogenic doses of BaP, although in the present case, DNA adducts could have accumulated from long-term exposure.

The suggestion originally made by us regarding the role of environmental contaminants in the aetiology of the single whale bladder carcinoma has since been further documented by the reporting of additional tumors in other whales from the same population. In particular, we described a focal haemangiomatous proliferation in a bladder mucosa, bearing similarities with the urinary bladder cancer reported earlier. Overall, from a first series of 15 necropsies, a total of six tumors were described from various tissues (Martineau et al. 1988). This incidence rate is nearly an order of magnitude higher than in similar studies of stranded cetaceans. Additional necropsies of St. Lawrence beluga whales (in progress) will help build up a larger sample for testing the significance of this finding.

We drew a parallel between the single whale bladder cancer case and the results of a human epidemiological study in the Saguenay area. Thériault et al. (1984) showed that the unusually high incidence of bladder neoplasms in workers in the area was associated with employment in the aluminium reduction plants, seemingly through exposure to BaP. Geraci et al. (1987) dismissed the human–whale comparison by pointing out that the association in workers is obscured by a history of cigarette smoking. However, Thériault et al. (1984) dissociated these two factors and showed that exposure to BaP through work in the reduction plant was the probable cause of the increased frequency of urinary bladder cancer. Additionally, they demonstrated an interaction between cigarette smoking and work in the aluminium industry in the generation of bladder cancer.

A high incidence of tumors in a whale population living in a highly contaminated area suggests that one or several environmental contaminants may be involved. Proposing a link between a powerful carcinogen found both in the environment and in the whales may be "simple," but it is also appropriate and logical — P. Béland, *St. Lawrence National Institute of Ecotoxicology, 310 des Ursulines, Rimouski, (Qué.) G5L 3A1*, and D. Martineau, *Department of Avian and Aquatic Animal*

Medicine, NY State College of Veterinary Medicine, Cornell University, Ithaca, NY 14853, USA. (J9667)

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Reply to Béland and Martineau

We do not dispute the diagnosis of transitional cell carcinoma in the whale. In fact, the description was precise and clear in essential details. Our point is that for this particular finding, it is scientifically unacceptable to implicate, as a cause, a substance that could not be detected. Information on benzo-α-pyrene (BaP) adducts in other whales was not published at the time of our writing, and has no direct bearing on this particular case.

Referring again to our common literature source, the data reviewed by Picard-Bérubé and Cossa (1983) show that BaP concentrations in other aquatic systems are within the range and up to 50 times higher than in the Saguenay estuary. Our statement should not be taken to suggest that such levels are acceptable, only that they are comparable.

When preparing our report, we reviewed the study by Thériault et al. (1984) and found that the odds ratio of 2.80 for nonsmokers exposed to BaP, with such a wide 95% confidence interval (0.25–32.02), is statistically indistinguishable from that for unexposed nonsmokers (1.00). Others who have reviewed the subject (IARC 1984) concluded that exposure to BaP presents only a borderline risk for nonsmokers. The influence of smoking is unequivocal.

We commend the subsequent study by Martineau et al. (1988) in which five additional tumors were found in 13 whales. The prevalence is higher than our finding of 10 tumors in 41 white-sided dolphins (Geraci et al. 1987), but certainly not by "an order of magnitude." What both studies show is that detailed examinations tend to reveal a broader spectrum of lesions.

The St. Lawrence River and many other aquatic habitats are contaminated with harmful substances, and every effort must be made to reverse this trend. The eventual process will involve an integrated effort by scientists, industry and government. Our responsibility as scientists is to provide sound, defensible evidence. However tempting the urge, to attribute an etiology to a single case on the basis of circumstantial evidence erodes our credibility and undermines that effort — J. R. Geraci, *Wildlife Diseases Section, Department of Pathology, Ontario Veterinary College, University of Guelph, Guelph, Ont. N1G 2W1*, N. C. Palmer, *Veterinary Laboratory Services, Ontario Ministry of Agriculture and Food, P.O. Box 3612, Guelph, Ont. N1H 6R8*, and D. J. St. Aubin, *Wildlife Diseases Section, Department of Pathology, Ontario Veterinary College, University of Guelph, Guelph, Ont. N1G 2W1.* (J9777)

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